

TRANSACTIONS
OF THE
ROYAL SOCIETY OF SOUTH AFRICA.

VOLUME XXVIII.
1941.

WITH FIFTY-EIGHT PLATES.

CAPE TOWN:
PUBLISHED BY THE SOCIETY.

—
1941.

STATE OF
VERMONT

... ..

CONTENTS.

	PAGE
A LIVING COELACANTHID FISH FROM SOUTH AFRICA. By J. L. B. SMITH. (With Plates I-XLIV and twenty Text-figures) . . .	1
A METHOD OF CORRECTING AN OBJECTIVE NOISE METER FOR USE ON COMPOSITE TONES. By R. GUELKE, Ph.D. (Communicated by B. L. GOODLET.) (With ten Text-figures) . . .	107
A STONE BEAD INDUSTRY OF THE WESTERN TRANSVAAL. By HAROLD S. HARGER, F.G.S. (With Plates XLV-XLIX and five Text-figures) . . .	129
ELECTRO-MAGNETIC INDUCTION IN WATER. By H. D. EINHORN, Dr. Ing. (Communicated by E. NEWBERRY.) (With eight Text-figures) . . .	143
A PRELIMINARY ACCOUNT OF RAINFALL IN JONKERSHOEK. By C. L. WICHT, Forest Research Officer. (With four Text-figures)	161
SPARID FISHES FROM PORTUGUESE EAST AFRICA, WITH A NOTE ON THE GENUS <i>GYMNOCRANIUS</i> KLUNZINGER. By J. L. B. SMITH. (With Plate L and three Text-figures) . . .	175
ORIENTABLE MANIFOLDS CONSTRUCTED FROM A SOLID CUBE. By D. B. SUMNER. (Communicated by A. BROWN) . . .	183
SILLIMANITE-CORUNDUM ROCK: A METAMORPHOSED BAUXITE IN NAMAQUALAND. By C. B. COETZEE. (Communicated by A. W. ROGERS.) (With Plate LI and one Text-figure) . . .	199
THE OCCURRENCE OF BARITE IN AN IRON ORE DEPOSIT IN NAMAQUALAND. By MORNA MATHIAS. (Communicated by A. W. ROGERS.) (With three Text-figures) . . .	207
THE RECENT ARCHÆOLOGY OF GOKOMERE, SOUTHERN RHODESIA. By T. GARDNER, S.J.; L. H. WELLS, M.Sc., M.B., Ch.B.; and J. F. SCHOFIELD, A.R.I.B.A. (With ten Text-figures) . . .	219
A PRELIMINARY INVESTIGATION OF THE IMPORTANCE OF DESICCATION, TEMPERATURE AND SALINITY AS FACTORS CONTROLLING THE VERTICAL DISTRIBUTION OF CERTAIN INTERTIDAL MARINE GASTROPODS IN FALSE BAY, SOUTH AFRICA. By G. J. BROEKHUYSEN, Ph.D. (Department of Zoology, University of Cape Town). (With Plates LII and LIII, and six Text-figures) . . .	255

	PAGE
NEW FOSSIL PIG REMAINS FROM THE VAAL RIVER GRAVELS. By J. C. MIDDLETON SHAW, Department of Dentistry, and H. B. S. COOKE, Department of Geology, University of the Witwatersrand, Johannesburg. (With Plate LIV and one Text-figure) . . .	293
A FOSSIL HORSE FROM KOFFIEFONTEIN, O.F.S. By L. H. WELLS, Lecturer in Anatomy, University of the Witwatersrand, Johannesburg. (With Plate LV and one Text-figure) . . .	301
THE COMPARATIVE ANATOMY OF THE TYMPANIC BULLA AND AUDITORY OSSICLES, WITH A NOTE SUGGESTING THEIR FUNCTION. A PAPER FROM THE UNIVERSITY OF CAPE TOWN. By J. A. KEEN (Department of Anatomy, University of Cape Town) and C. S. GROBELAAR (Zoological Institute, University of Stellenbosch). (With seventy-eight Text-figures)	307
THE LIFE-HISTORY OF <i>CYCLOGRAPSUS PUNCTATUS</i> , M. EDW.: BREEDING AND GROWTH. By G. J. BROEKHUYSEN, Ph.D., F.A.G.S., Department of Zoology, University of Cape Town. (With Plates LVI, LVII, and eleven Text-figures)	331
FACTORIAL ANALYSIS AND SCHOOL SUBJECTS: A CRITICISM. A Paper from the University of Cape Town. By H. A. REYBURN and J. G. TAYLOR	367
THE VASCULAR ANATOMY OF <i>XENOPUS LAEVIS</i> (DAUDIN). By NAOMI MILLARD, M.Sc., Department of Zoology, University of Cape Town. (Communicated by T. A. STEPHENSON.) (With twenty Text-figures)	387
THE GENUS <i>GYMNOCRANIUS</i> KLUNZINGER, WITH NOTES ON CERTAIN RARE FISHES FROM PORTUGUESE EAST AFRICA. By J. L. B. SMITH. (With Plate LVIII and one Text-figure)	441
SOME ECOLOGICAL FACTORS AFFECTING THE FERTILITY OF TROUT EGGS AT THE JONKERSHOEK TROUT HATCHERY. By D. HEY, M.Sc. (Communicated by A. J. H. GOODWIN.) (With one Text-figure, eight Graphs, and one Table)	453

TRANSACTIONS

OF THE

ROYAL SOCIETY OF SOUTH AFRICA.

VOL. XXVIII.

A LIVING COELACANTHID FISH FROM SOUTH AFRICA.

By J. L. B. SMITH.

(With Plates I-XLIV and twenty Text-figures.)

(Read June 21, 1939.)

TABLE OF CONTENTS.

	PAGE		PAGE
INTRODUCTORY	2	PREOPERCULAR FLAP	24
FAMILY COELACANTHIDAE	4	PREOPERCULAR APPARATUS	24
GENUS <i>Latimeria</i>	6	PREOPERCULAR	24
<i>Latimeria chalumnae</i>	10	SQUAMOSAL	25
Vent	11	POSTORBITAL	26
FINS	11	LACRIMO-JUGAL	27
First Dorsal	12	QUADRATO-JUGAL	29
Second Dorsal	13	CIRCUMORBITALS	29
Anal	13	SENSORY CANAL INNERVATION IN	
Pectorals	13	THE CHEEK-BONES	29
Pelvis	14	FRONTO-ROSTRALS	29
Caudal	14	FRONTAL (1)	30
TERMINAL PORTION OF VERTEBRAL		FRONTAL (2)	32
COLUMN	16	FRONTO-NASAL (3)	33
PECTORAL GIRDLE	17	ROSTRAL ELEMENTS (4, 7-10, 19)	33
CLAVICLE	19	Postrostral (4)	33
CLEITHRUM	19	Rostral (7)	33
EXTRACLEITHRUM	20	Rostral (9)	34
SUPRACLEITHRUM	21	Meso-rostral (8)	34
HEAD EXTERNAL	22	Inter-rostral (8')	34
OPERCULAR	22	Rostral (10)	34
SUBOPERCULAR	23	Rostral (19)	34
INTEROPERCULAR	23	PARAFRONTALS	34

	PAGE		PAGE
PARAFRONTO-ANTORBITAL	36	METAPTERYGOID	74
ROSTRALS (20, 21, and 22)	36	PTERYGOID	76
NASO-ANTORBITAL	37	AUTOPALATINE	77
ROSTRO-NASAL	38	ECTOPTYERYGOID	78
INNERVATION OF THE PARAFRONTAL		ECTETHMOID	78
CANAL	38	PREVOMER	80
LATERAL ROSTRO-NASAL	39	PARASPHENOID	80
INTERTEMPORALS	40	HYOMANDIBULAR	82
SUPRATEMPORALS	41	SYMPLECTIC	84
POSTSPIRACULAR	42	FRONTO-INTERTEMPORAL JOINT	85
EXTRASCAPULARS	42	PROOTIC	86
SENSORY SYSTEM	44	PROOTIC OSSICLE	88
Occipital Region	45	CHONDROCRANIUM	89
Supratemporal Canal	47	BRAIN CAVITY	91
Parafrontal Canal	47	BASISPHENOID	91
Rostral Commissurals	49	RESPIRATORY ORGANS	92
Infraorbital Canal	52	Spiracle	92
Jugal and Preopercular Canals	53	Gills	93
Mandibular Canal	54	SPIRACULAR POUCH	94
OLFACTORY ORGANS	54	ANTOTIC CAVITY	94
ROSTRAL TENTACLE	58	POSTSPIRACULAR GROOVE	95
STRUCTURE OF MANDIBULAR RAMI	58	SQUAMATION	95
ANGULAR	59	SCALE COUNTS, ETC.	97
SPLENIAL	60	LATERAL LINE	100
ARTICULAR	60	LATERAL LINE SCALES	100
GULAR	61	FLESH AND MUSCULATURE	102
CORONOID	62	OIL	103
MOUTH	62	STRUCTURES OF UNCERTAIN IDENTITY	103
LOWER JAW	63	Muscle Sheath	103
COPULA	66	Palatine Canal	103
UPPER JAW	68	HABITAT	104
STRUCTURE OF DENTAL PLATES AND		PLATES I-XLIV	at end
OF TEETH	72	FOLDER-PAGE I	at end
PALATO-PTERYGO-QUADRATE SYSTEM	73	FOLDER-PAGE II	at end
QUADRATE	73		

INTRODUCTORY.

For the benefit of the numerous workers who are interested in primitive fishes, and to whom this recently discovered specimen is inaccessible, the preparation of a descriptive account has been pressed forward with as little delay as possible.

This has been accomplished under the chief handicaps of lack of time and of any but relatively crude equipment. Also I have constantly been torn between my desire to give all possible information, and a natural reluctance to dissect or remove structures from so unique a specimen not my own. Further, the task has been rendered the more difficult by the treatment the specimen had undergone. It has been most aggravating to

work with the remains of rudely torn structures, the least of which would have been of inestimable scientific value.

Throughout this work clear distinction is drawn between facts about complete structures and suppositions based upon fragmentary remains or defective parts.

With the chief aim of providing early information, it has been possible to give only the briefest attention to even the more obvious of the many important and interesting sidelights shed by this specimen upon taxonomic problems and upon the nature of fossilised structures. For the same reason it has not been possible to carry out continued polishing of the phrasing of the text, and the text-figures presented are not as finished as they might be, though they are as accurate as repeated observation and measurement can make them. My investigations into the remaining parts of the occipital region have not been so exhaustive as for other structures, since public clamour for view of the specimen curtailed the time it was available to me.

I wish to record here my gratitude to Miss Courtenay-Latimer and to the Board of Trustees of the East London Museum for having entrusted the specimen to my care for over two months, to enable me to carry out my investigations in Grahamstown. This generosity is very greatly appreciated.

An account of the circumstances attending the discovery of the specimen has previously appeared (Smith, *Nature*, 1939, vol. cxliii, p. 455). It has been explained how a delayed letter was primarily responsible for the tragic loss of the carcass.

To Captain Goosen, who was originally responsible for saving the specimen, I am indebted for most of the details contained in the following description of the conditions attending the catch. The 22nd December 1938 was a normal fine day without high wind. The inshore course of the Mozambique current was normal, *i.e.* from the north-east, more or less parallel with the coast, and of a speed of 1-2 knots at 2-3 miles offshore. Within that belt reverse inshore eddies are sometimes found. The trawl was shot at a point about 3 miles offshore in approximately 37 fathoms, some 18 miles south-west of East London, near the mouth of the Ohalumna River. The course was at first north-east for about 3 miles. The vessel then circled around an elliptical area of major axis about 6 and minor about $3\frac{1}{2}$ miles, the long axis set roughly N.W. and S.E., with closest approach to the shore of just less than 2 miles. The centre of this area lies approximately 5 miles offshore, roughly south-west of East London, at $33^{\circ} 12' \text{ S.}$ and $27^{\circ} 46' \text{ E.}$ The net was hauled aboard at the close of the ellipse, some 3 miles offshore, in just less than 40 fathoms.

This area is but seldom trawled, since fishes are not commonly found

there. In the trawled area the bottom is composed variably of mud or sand, with pebbly stretches. Immediately to the east of the trawled area is a roughly circular patch of about $2\frac{1}{2}$ –3 miles in diameter, of depth 40–46 fathoms, with a bottom of rocky reefs where trawl-nets cannot operate. I hesitate to name this latter as the probable habitat for the Coelacanth, since line-boats frequent that neighbourhood. The area where the catch was made is the inshore portion of a gently inclined shelf 9–11 miles in width, which slopes gradually seawards from 40–60 fathoms of depth. The edge is apparently abrupt, depths of 120 to over 200 fathoms being recorded just beyond the shelf. I have no information about the nature of the bottom at the edge of that shelf, but consider it very probably to be a rocky ridge. Such conditions represent a most likely habitat for the Coelacanth.

When the net had been hauled aboard and the "cod-end" slipped, 3–4 tons of various fishes lay piled on deck. Most of the fishes in any considerable haul are dead by the time they reach the deck of the trawler, certainly those more delicate forms from deeper water. The sorting of the heap in this case took about 30 minutes, and only at the bottom was the Coelacanth observed. It attracted the notice of the captain, who decided to preserve it for the East London Museum. Despite all that it had endured the Coelacanth was alive, and so vigorous as to be aggressive, snapping viciously at nearby hands. It showed signs of life for at least 3 hours after its discovery, *i.e.* $3\frac{1}{2}$ –4 hours after removal from the water—a point of significance in connection with its probable habitat.

It is again emphasised that this paper is primarily descriptive, although a certain degree of conjecture and deduction is unavoidable. As far as possible the facts are set forth without relation to zoological polemics, and the nomenclature adopted is in most cases arbitrary. This is particularly the case with the fronto-rostral series of bones. In this fish at any rate it is not easy to define any particular exclusively "frontal" or other neighbouring area where those bones are placed. For that reason most of those ossicles are usually referred to by the numbers assigned in the notation employed.

For convenience and uniformity, throughout all the illustrations each structure is labelled with the same figure or letter. A key to all the symbols employed is given in Folder-page I at the end of the paper.

FAMILY COELACANTHIDAE.

Stensiö, *Triassic Fishes*, Spitzbergen, 1921, p. 120.

Until a complete specimen becomes available for examination it is hardly advisable to attempt a full revised diagnosis of the family, since

in some respects fossil remains are more complete than the specimen now described. In so far as the features which remain in this specimen are concerned, Stensiö's description (*loc. cit.*) is in the main very accurate, and only brief emendations or additions are given below.

Spiracles present (probably functionless).

No internal narial opening of the mouth. A median rostral sinus with one rostral and two lateral external openings on each side. Olfactory capsules without external openings.

Hyomandibular system present (of which the opercular is a part), connected with the mandibular ramus by a "symplectic" bone which articulates with the articular behind the quadrate.

Maxilla and premaxilla absent. Marginal dental plates apparently modified cosmoid scales.

Parafrontal canal continuous with the infraorbital canal and with the rostral commissural canals.

An extracranial cavity within the pterygoidal column (see Spiracular Pouch and Antotic Cavity below), probably corresponding to the primitive condition of the *cavum epiptericum* of lower Tetrapoda.

The hyomandibular system suggests affinity with Palaeopterygian forms, e.g. *Polypteriidae* and the *Chondrostei*.

The basicranial structure, with the hinder part of the parasphenoid, had been removed and lost, so that the presence or absence of a myodome cannot be established. From the nature, rise and orientation of the remaining structures it appears likely that a structure corresponding to the myodome is present in this fish.

The *Coelacanthidae* are closely related to the *Rhipidistians*, and it appears to be generally accepted that the former have originated from the latter. There is as yet no irrefutable evidence on this point, nor any recognised transitional form. The Devonian *Diplocercides* v. Koenen is sometimes cited for this, but both that genus and the related *Nesides* Stensiö are undoubted *Coelacanth*s.

It is certainly true that the two groups show marked coincidence in structures not found in other fishes, and records at present show the earliest *Rhipidistians* to be older than any known *Actinistian* form. The *Coelacanth*s are supposed to have originated from the *Rhipidistian* ancestor partly by loss of the maxillary bones, with consequent modification of the bones of the cheek, also by loss or absorption of several of the more important dermal bones of the head, besides other changes.

There appears to be no satisfactory theory to account for the "loss" of the maxillary bones, nor to explain how such regression occurred. In the living specimen recently discovered the structure of the upper jaw hardly suggests modification due to the "loss" of the maxillary bones,

but rather that those bones were never present, having failed to develop in any ancestral form. The "pseudo-maxillarial" fold (G) found in this fish suggests that the maxilla of fishes originated by modification of some such structure, *i.e.* of a primitive dermal fold, and that in the Coelacanth and their ancestors the necessary modification (and ossification) did not occur. The great development of the coronoids in the lower jaw may be an accompaniment of the non-development of maxillarial bones. The general appearance of the upper jaw and rostrum in this Coelacanth suggests transition from a form with inferior or sub-inferior mouth, in which the pre-oral part of the snout has suffered reduction.

The Coelacanthidae are characterised by immutability in high degree. They are all known to have been very closely related in structure and form, and to have been perhaps the most tenaciously retentive of structure over vast periods of time of all Osteichthyes, possibly of all vertebrates. That particular character is very firmly established by the discovery of a living specimen, which has been found to contain structures practically identical with those of even Devonian forms, and to show more than ordinary correspondence with those of the Permian and the Triassic. The changes which are supposed to have produced the Coelacanth from the Rhipidistian form must have occurred in a relatively brief period of time, since both are there full-fledged, not widely separated in Devonian times. Even allowing that evolutionary changes in those times may have occurred with unusual speed, it seems remarkable that such rapid and relatively profound changes (*i.e.* Rhipidistian to Actinistian) should have ended so abruptly in the relatively immutable, virile, generalised Coelacanthidae.

It is possible that the character of at most slow structural modification has always been typical of the Coelacanthid line, and that those fishes contain structures but little modified from those of even remote ancestors. Possibly the recently discovered aberrant nasal structures may even indicate some affinity with early agnathate vertebrates, which in degree is indicated also by the nature of the upper jaw. That the Coelacanthidae and the Rhipidistians had common ancestry is very probable. That the latter gave rise to the former would appear to require more definite evidence.

Genus *Latimeria* J. L. B. Smith.

Smith, Nature, 1939, vol. cxliii, p. 455 (provisional designation); *ibid.*, vol. cxliii, p. 748.

Smith, Trans. Roy. Soc. S.A., 1939, vol. xxvii, p. 47.

Very large fishes. Body robust, moderately compressed, elongate-oval. Scales cycloid, large, mostly longer than high, with exposed surface sub-rhomboid, surface ornamentation in the form of elongated tubercles or

spines, arranged usually in caudally radiating rows. A single lateral line present, complete to the end of the supplementary caudal. Lateral line tubes bifurcate.

Mouth fairly large, terminal. Maxillae and premaxillae absent. Marginal dentition of upper jaw in the form of dental plates, below rostrals, prevomers, palatines, and ectopterygoids. Dentition primarily raptorial. Teeth all conical, chiefly small, numerous isolated pairs of large tusks. Teeth in dermal plates on lower lips, dentaries, prearticulars, coronoids, rostrals, prevomers, palatines, pterygoids, ectopterygoids, and parasphenoid. Gulars large.

Head large, fairly broad. Prootic large, presumably paired, latero-posteriorly overlapped by and attached to the infero-antrorse process of the supratemporal, over which is bound a capsular process (92). Antotic process and probably also the body of the basisphenoid lightly ossified, cancellate.

A strong, lateral ectethmoidal ossification (38) connecting the palatoquadrate system anteriorly with the parasphenoid and the chondrocranium. The olfactory capsule lies within and anterior to this structure. Parasphenoid large and wide with lateral margins folding dorsally, forming a deep trough bearing the base of the anterior chondrocranium. Brain extending far forwards.

Pterygoid with long, low, anterior limb without notch in its dorsal margin. Autopalatine overlapping the anterior extremity of the pterygoid. Posteriorly the pterygoid has a high lobe, with superiorly the metapterygoid, and inferiorly the quadrate firmly attached to, apparently ankylosed with, the outer face.

Angular long and low, splenial short, both with ganoin-covered exposed portions. Articular short with supero-posterior facet for base of symplectic. Coronoid trapeziform, longer than high, with basal granulate plate. Hyomandibular system of a symplectic articulating inferiorly at the hind end of the articular, supero-obliquely with a central capsular hyomandibular ossification bound to the inner anterior face of the opercular. Hyomandibular elongate with lower and upper cartilaginous portions, the upper enveloping the opercular-supratemporal articulation.

Main sensory canals of the head rather wide. Parafrontal canal only not in tubular bone, but carried between bilaminar articulating fronto-rostral and parafrontal series. Preopercular canal continuous in skin of hinder lower cheek with mandibular canal. A lateral rostro-nasal carrying a canal into which join the parafrontal, the infraorbital, and the rostral commissural canals.

Cheek plates four or five in number, being a postorbital, a suborbital, either a single squamosal or the latter in two parts, as squamosal and suprasquamosal, and a preopercular. Cheek plates articulating posteriorly

to form a "preopercular" system. The four main cheek plates primarily sensory canal bones, circumorbital plates probably absent. Quadratojugal absent or obsolescent. Subopercular and interopercular present but not fully developed. Opercular fairly large, subtriangular, with upper anterior corner articulating with supratemporal. Supratemporal moderate, intertemporal large, joined by moderate suture. Both bones with ganoin-covered areas exposed above the skin. None of the dermal bones much ornamented. The opercular with posterior tubercles.

Extrascapulars four on each side with median connecting unit, reduced to mere tubules or roofing laminae.

Fronto-rostral series of bones lamino-radiate, marginally sutured or articulated, anteriorly with large apertures as pores of the sensory canal system. The main frontal with an infero-posterior process which has the position and function of an alisphenoid.

Gill-openings wide and unrestricted. Opercular membranes of thick wrinkled skin, free from isthmus. Gills 4, spinescent. A tuberculate copula present as a roofing structure to basihyal and to basibranchials. Hyoidean gill-slit probably present. Spiracles present, small, situated laterally below the fronto-intertemporal joint, with lateral groove and posterior ossicle.

Supplementary caudal present. Rays of all fins, except pelvics, partly or fully, weakly or strongly spinescent. Pelvics abdominal, inserted below between the two dorsals. First dorsal short, of 8 robust spiny ossified rays, with posterior membrane. Pectorals, pelvics, anal, and second dorsal fins pedunculate-lobate, scaling far along the lobe. All rays hollow, composed of two lateral segments, and but little expanded distally, finely articulated for almost the entire length.

A central sinus in the mesethmoidal region of the chondrocranium which opens externally through three tubes on each side, one rostral and two antorbital. This organ is not connected with the olfactory capsules, each of which lies within the ectethmoid bone (38) covered anteriorly by the lateral rostro-nasal. The olfactory sacs without external opening. No internal nares in the mouth.

Vertebral column acentrous, notochord persistent, with cartilaginous sheath, to which the neural and haemal arches and spines are probably attached. (No other endoskeletal parts of fins remain.) Extracleithrum present. Supracleithrum a separate ossification.

Air-bladder presumably unossified. (The taxidermist stated that all of the endoskeleton was soft, presumably cartilaginous. I do not consider that can be correct. The few odd portions I have seen, *e.g.* a haemal spine, are only lightly ossified, but they are ossified. The basal plates of the fins were surely well ossified as in other forms.)

Genotype.—*chalumnae* J. L. B. Smith.

Type.—A stuffed specimen in the East London Museum.

I have attempted to prepare a systematic key to the genera of the Coelacanthidae to show the taxonomic relationships of *Latimeria*. With the necessarily incomplete data available it does not appear possible to evolve anything of systematic value.

All the genera are rather closely related. The more primitive show a greater degree of endocranial ossification than those of the Mesozoic, but the remaining known structural differences are generally not of very great taxonomic significance. It is remarkable that all genera and species have the typical form and major characteristics which place the Coelacanthids in a class apart. The present specimen is in every respect a typical member of that family, and shows structural affinities with practically every fossil genus. It is most closely related to those which are recorded from the Carboniferous to the Triassic, and might indeed be placed in several of them. However, it differs from any one by features at least as significant as those which are held to distinguish any two related existing genera.

Originally, when my knowledge of the Coelacanthids was superficially systematic only, I considered *Latimeria* to lie very close to *Macropoma* Agassiz, the only genus of which I then had any detailed account. *Latimeria* is, however, more closely related to the Carboniferous *Rhabdoderma* Reis, and to the Triassic genera *Wimania* Stensiö, *Azelia* Stensiö, *Whiteia* Moy-Thomas (and to the imperfectly known *Sassenia* Stensiö, with which *Whiteia* is probably identical). It is possible that *Latimeria* appears to diverge more widely from some of the remaining genera because they are only imperfectly known.

From *Rhabdoderma*, *Latimeria* is distinguished by the lesser extent of the dermal bones of the head, by the lesser degree of ossification of the endocranium, as well as by the presence of denticles on the lepidotrichia.

From *Whiteia* (known from Greenland and Madagascar), *Latimeria* is distinguished by the nature and extent of the dermal bones of the head, and of the extrascapulars; also by the type of ornament on the scales and head.

From *Wimania*, *Latimeria* differs chiefly in the type of ornamentation on the scales, in the character of the parafrontal sensory canal, and in the nature and arrangement of the cheek plates.

From *Azelia*, *Latimeria* is distinguished by the nature of the canal-bearing bones of the cheek, by the dentition, and by the notched dorsal margin of the pterygoid of the former.

Both *Wimania* and *Azelia* have the alisphenoidal-infero-posterior limb to the frontal, which extends behind the fronto-intertemporal joint

to form a junction between the dorsal face of the antotic process of the basisphenoid and the ventral face of the inner lateral margin of the intertemporal (*q.v.*).

What I observe in this specimen of *Latimeria* indicates that the founding of even new species upon variations in fragmentary remains is venturesome. There is not even perfect bilateral symmetry in this one specimen (see Squamosal, and Lateral Line Scales, below). There is likely to be fairly wide variation, especially in external structures, between individuals, certainly among adults, in any one species.

Latimeria chalumnae J. L. B. Smith.

Smith, Nature, 1939, vol. cxliii, p. 455 (provisional designation); *ibid.*, vol. cxliii, p. 748.

Smith, Trans. Roy. Soc. S.A., 1939, vol. xxvii, p. 47.

From what can be ascertained, the body did not suffer any appreciable degree of distortion during mounting, save perhaps slight elongation.

Body elongate, oblong-oval, fairly robust, moderately compressed. The body is thickest at the shoulder and tapers posteriorly very gradually to below the middle of the principal caudal rays, thence rapidly to the supplementary caudal (Plate XIII). The head is not quite as broad as the body. The dorsal profile is almost smooth, fairly gently convex from before the dorsal origin to the snout, with a faint supraorbital prominence at the fronto-intertemporal joint (Plates I, XIV, and XV).

Total length of body to end of supplementary caudal 1500 mm. Depth of body just behind pectoral base, almost uniform to below middle of first dorsal, 370 mm. Depth just behind base of pelvis 345 mm., at origin of second dorsal 295 mm. Width of body behind pectorals 190 mm., in advance of first dorsal 160 mm., just in advance of dorsal principal caudal rays 85 mm.

Length of head in profile from tip of snout to hind margin of opercular membrane 390 mm. Depth of head through anterior margin of opercular plate 250 mm., through hind margin of opercular plate 315 mm. Width of head in profile between upper margins of opercular plates 145 mm. Total width of head across front of opercular plate 168 mm. Maximum width of head across spiracles 155 mm., across centre of eye 150 mm.

Snout in profile 68 mm., measured obliquely 98 mm. Longitudinal diameter of orbit 56 mm., vertical diameter 52 mm. Centre of eye slightly nearer (in profile) snout tip than hind margin of squamosal (24). Centre of eye 2.6 times farther from ventral than from dorsal profile. Hind margin of eye to anterior margin of opercular plate 102 mm., to hind margin of opercular membrane 270 mm.

Interocular space 111 mm. Least depth of suborbital (lacrimo-jugal, 48) 21 mm. Vertical distance between lateral nostrils 16 mm. Lower nostril (B) 8 mm., upper (C) 7 mm. in longitudinal diameter. Upper internarial distance 82 mm., lower internarial distance 99 mm. Distance between rostral narial openings (A) on snout tip 34 mm. Distance from spiracles to snout tip 180 mm. Interspiracular distance 72 mm. Distance from snout tip to the fronto-intertemporal joint 175 mm. Distance from snout tip to hind margin of external pseudo-maxillarial labial fold (G) 145 mm. Total width of mouth at outer margin of pseudo-maxillarial labial fold 180 mm. Width of lower jaw across anterior coronoids (40) 135 mm. Total width of rostrals 55 mm. Total length of mandible 250 mm. Gulars (31) originate 42 mm. behind the tip of the lower jaw at symphysis. Length of gular 225 mm. Maximum width across gulars 132 mm. Distance from snout tip along dorsal profile to origin of scaling on nape 280 mm. Snout tip to first dorsal origin along profile 620 mm., to second dorsal origin 920 mm. Distance from snout tip to anterior margin of pectoral base (in profile) 340 mm., to origin of pelvis 630 mm., to origin of anal 960 mm.

Vent.—The vent appears to have been situated about 80 mm. in advance of the insertion of the anal fin. Unfortunately, the fish had been slit open along the mid-line of the belly, and the repairs render it impossible to decide the exact location of the vent. The taxidermist was unable to assist me in this matter.

There is now no trace of any intromittent organ, nor could any have been present unnoticed. If vivipary in *Coelacanth*s is accepted, this specimen is likely a female. Its size appears to confirm this.

FINS.

(Plates I, II, III, IV, V, VI, VII, VIII, XIII, XIV, XV.)

The paired fins, the second dorsal, and the anal fin are all pedunculate-lobate. They have stout columnar bases, dilating over the point of attachment to the body. Apically they are compressed into a lobe wider than the peduncle, the rays fringing the margin of the lobe. The rays in these lobed fins are rather slender and but little ossified in the exposed parts. They are all only very slightly dilated in the distal portion, if at all. The pelvis only are quite smooth. The rays of the other lobed fins bear some ornamentation in the form of denticles.

The first dorsal and the caudal fins are normal—not lobate. The rays in those fins are, especially anteriorly, heavy and strongly ossified, and heavily armoured with strong spines and tubercles. The degree of ossification and the ornamentation diminish posteriorly and distally. There is some degree of basal scaling for the first dorsal and the caudal fins.

All rays in all fins are articulated. Even in the strongly ossified rays the articulations may be traced far down the structure. The articulations are generally fine and fairly close-set (Plate XXIX).

All rays are composed of two lateral segments, each of which is transversely concave, held together by thin connective tissue. Thus for the greatest part the basal subcylindrical portion of each ray is a hollow cylinder containing cartilaginous tissue. Even the more distal compressed portions have the same structure, though the internal cavity is elongate-oval in cross-section. The membrane connecting the rays is continuous with that binding the ray segments together.

First Dorsal.—First dorsal with 8 rays, practically no scaly basal sheath (Plates I and II), inserted above the end of the first third of the body almost exactly twice as far from the tip of the supplementary caudal as from the tip of the snout. All the rays of the first dorsal are to some extent ossified, though clearly articulated well down into the bony portion. A longitudinal median suture in the first ray shows clearly for the whole length. Dense ossification extends almost the whole length of the first ray, and diminishes progressively posteriorly, the last ray being soft in its distal third. The membrane (now damaged) is thick, and had apparently extended to the tips of the rays with little emargination. Behind the fin the membrane was continued as a flap joined to the back (Plates I and II).

All rays are laterally denticulate, the anterior strongly so. The first ray is very stout, with the basal denticles in several series worn to blunt tubercles. Higher up the ray the denticles are stout but sharp, in two series on each side directed mainly obliquely upwards, and extending to the tip of the ray (extreme tip broken and lost). The second ray (damaged) is slightly less stout than the first, is naked for 15 mm. basally, and bears denticles for almost its entire length. A few of the basal spines are blunted, and for most of its length the ray bears three series of denticles directed at all angles, but chiefly slightly obliquely upwards. The third and fourth rays are of equal thickness, slightly less robust than the second. They are naked for 10 mm. at the base, and the denticles commence irregularly as a single or double series, increasing to two or three rows distally. About nine-tenths of the third ray and about seven-eighths of the fourth ray are strongly ossified, but small denticles continue as a single series on the soft portion. The fifth ray is slightly less ossified distally than the fourth. The denticles are smaller, chiefly directed obliquely upwards, and commence about 15 mm. above the body as a single series of fine points along the distal unossified portion to the tip. Only three-fourths of the sixth ray is strongly ossified, and it is somewhat more slender than the fifth. It bears denticles of form and arrangement similar to those on the fifth ray. The seventh ray is shorter and more slender than the sixth, and densely

ossified for only two-thirds basally. The basal 20 mm. is edentate, and the denticles originate as a single series, becoming double for only a very short distance medially, thereafter continuing as a single series of fine points to the apex. The eighth ray is much the smallest and the most slender. Dense ossification extends for the basal two-thirds, and the denticles are upwardly directed, arranged much as those on the seventh ray, but are much smaller.

Base of dorsal rays 76 mm., total base of first dorsal 230 mm. First dorsal ray (damaged) 128 mm., second (damaged) 135 mm., third 165 mm., fourth 168 mm., fifth 163 mm., sixth 155 mm., seventh 134 mm., and eighth 104 mm. in length.

Second Dorsal.—Second dorsal with 30 rays (Plates I and III) originates above 1.2 times farther from the snout tip than from the end of the supplementary caudal, about midway between the latter point and the middle of the preopercular. The oval base is 62 mm. in transverse diameter (minor axis) and about 105 mm. longitudinally. The fin is directed obliquely backwards, peduncle scarcely bent, at an angle of about 45° . Distance from base to highest margin of scaling 185 mm. Transverse width of peduncle 50 mm., greatest width across scaled lobe 64 mm. Twelfth and thirteenth rays longest, free length beyond scaling 92 mm. Rays fairly slender, only the median (longest), from the ninth to the nineteenth, show a slight degree of distal dilation. The last rays, twenty-fourth to thirtieth, become progressively finer. All the rays are laterally compressed, *i.e.* elongate-oval in cross-section, with fine, close-set articulations the whole free length. The fourteenth to the twenty-first ray inclusive have a few small denticles on the base of the exposed portions in a single series. These are better developed on the right side, but distinct on both.

Anal.—Anal with 29 rays, originates 1.6 times farther from snout tip than from end of supplementary caudal, midway between the latter and the pectoral axil. The oval base is 60 mm. in transverse diameter, about 75 mm. longitudinal diameter. The fin is directed obliquely backwards, lobe bent upwards at an angle to peduncle (Plate I). Distance from body at base to farthest extent of scaling 175 mm. Transverse width of peduncle 50 mm., greatest width across scaled lobe 55 mm.

Twelfth ray longest, free length beyond scaling 92 mm. Rays compressed, fairly slender, little if at all dilated distally. They are more compressed distally, and finely and closely articulated all the free length, in structure exactly as the dorsal rays.

A few basal spinules or tubercles on the mid-rays. Tip of anal lobe reaches to base of third principal ventral caudal ray.

Pectorals.—Pectorals with 32 rays, elongate (Plates I, VII, XIII, XIV,

XV). Peduncle fairly short. Total length from body for right pectoral 330 mm., left 300 mm. Twelfth to fourteenth rays longest, extend 135 mm. beyond scaling. Peduncle 45-55 mm. in width, scaling on flattened lobe 70 mm. wide at widest point. The anterior pectoral rays only moderately compressed basally (beyond scaling), more compressed distally.

From the third to the seventeenth, on the outer surface only, the rays bear a single series of rudimentary spinules or granules which resemble the tubercles on the scales. The lower surface of those rays (*i.e.* against the body) is quite smooth, only one or two slight tubercular irregularities being apparent. The remaining rays are smooth. The tips of the pectorals reach to the base of the pelvics.

Pectorals inserted with upper margin of base slightly below middle of side, and hind margin of base just below the hind margin of the opercular membrane. The front of the base is largely covered by the heavy opercular membrane. The fin is distinctly falcate in outline.

Pelvics.—Pelvics with 33 rays, inserted 1.4 times farther from the tip of the supplementary caudal than from the tip of the snout, immediately behind the base of the last ray of the first dorsal (Plates I, VIII, and XIII). Total length from body 260 mm. (left pelvic), the right is damaged and is sewn closer to the body. Peduncle fairly short and depressed (dorso-ventrally). Longitudinal width of peduncle 65 mm., vertical depth 40 mm. Length from body to apex of scaling on lobe 150 mm., greatest width of scaled lobe 75 mm.

Fin more or less symmetrically fringed, unlike other lobate fins, which are falcate or subfalcate. The fourteenth ray is the longest, free margin beyond scaling 116 mm. Rays moderately compressed at base, apically more strongly, and closely and finely articulated for entire free length. No sign of spinules or granules on rays, which are quite smooth.

Caudal.—Caudal geophycocercal with protruding axial supplement and very little scaly basal sheath (Plates I, IV, and V). Rays $25 + 38 + 21$. The dorsal principal caudal rays originate slightly in advance of the lower, above 3.2 times farther from the snout tip than from the hind margin of the supplementary caudal, above the 58th lateral line scale.

The caudal peduncle is robust and fairly compressed. Depth of narrowest portion 210 mm., width 105 mm. From the narrowest part the caudal widens, and at the point of origin of the dorsal caudal rays the depth is 235 mm. Across the point of origin of the ventral caudal rays the depth is 250 mm., thereafter the caudal is cuneate and tapers very rapidly to the base of the supplementary caudal (Plates I and IV). In thickness the caudal tapers very gradually, almost imperceptibly, to behind the origin of the principal rays, thereafter very abruptly to the base of the supplementary caudal (Plate XIII).

The 25 dorsal principal caudal rays resemble those of the first dorsal. Anteriorly they are thickened and ossified, decreasingly so posteriorly. All the rays show the median suture observed on the rays of the first dorsal, and are strongly spinose. The first ray is short, 60 mm. free length above scaling, and is completely ossified. It is strongly spinate on the anterior margin and laterally to the tip. The spines are very stout in two main series anteriorly, mostly directed upwards, some almost hook-like. Laterally on each side there is one main irregular series to the tip. Second ray 130 mm. in length beyond basal scaling, only the extreme tip soft, though articulations are visible down into the bony portion. The ray thickens upwards from the base, and is stoutest about the middle of its length. Beyond the tip of the first ray there are on the front of the second ray two rows of upwardly directed stout spinules, one on each side of the median suture, extending to the tip. There are approximately 31 in each row from the tip of the first ray to the apex of the second. Basally the second ray bears two series of similar robust denticles which gradually diminish distally to a single lateral row. The third ray extends beyond the basal scaling about 140 mm., and is soft only at the extreme tip, although, as in the dorsal rays, articulations are visible for a considerable distance down the ray. On this and on the succeeding rays the denticles are confined to the sides. A double series, somewhat irregular, extends from the base to the apex, approximately 37 in each row. The fourth ray is 135 mm. in length beyond the basal scaling, and bears somewhat sharper and more slender upwardly directed denticles which extend to the apex. The fifth and succeeding rays are less robust, and somewhat though comparatively irregularly more widely spaced than the anterior four, whose bases are contiguous. Length of fifth ray beyond basal scaling 130 mm. It bears two lateral series of fairly acute upwardly directed denticles which extend to the apex, as a single series of diminished size on the soft portion of the ray. The sixth ray, 125 mm. beyond the basal scaling, is very similar to the fifth. The seventh to tenth rays are approximately subequal in free length, 115 mm. beyond the basal scaling. They are slightly more slender and apically less ossified than the sixth, each bearing a double series of upwardly directed acute spinules. The eleventh and twelfth rays are similar to the tenth, but slightly shorter, 100 mm. free length. Lateral spinules in two series, apically single. The remaining principal dorsal rays gradually diminish in length, thickness, and degree of ossification. The twentieth ray extends 80 mm. beyond the basal scaling, and is strongly ossified for only the basal third. The articulations are visible right down to the base, and the ray bears an irregular double series of moderate upwardly directed spinules for the basal two-thirds, becoming a single series apically. The remaining five rays are still shorter, the last being

60 mm. in free length. They are soft, and bear chiefly a single row of lateral spinules.

Length of base of dorsal principal caudal rays 300 mm. Margin of fin gently convex, membrane apparently extended to tips of rays in life. First ray approximately 5 mm., fifth 3 mm., and twentieth 2 mm. in thickness.

The 21 ventral principal caudal rays (Plates I, IV, and VI) originate behind the origin of the upper rays, below the 63rd lateral line scale. The rays resemble those of the dorsal portion of the fin, but the spination is more pronounced. The bases of the second to the fifth rays are adjacent. First ray very short and stout, almost like a ventral keel, 22 mm. in length, the free margin being parallel with the body outline. It bears a double series of 9 blunt tubercles. Second ray 55 mm. in length beyond basal scaling, with four rows of upwardly directed stout spines to apex. Third, fourth, and fifth rays are stout, almost completely densely ossified. The third ray has an anterior series of upwardly directed stout spines from beyond the apex of the second ray to the tip, laterally one to two series of similar spines to apex. Fourth and fifth rays with a double to treble series of stout spines laterally. Sixth ray slightly less robust than the preceding rays, but almost fully ossified. Free length beyond basal scaling 108 mm. From the seventh onwards the rays gradually become less robust and progressively less ossified, while the spination diminishes to denticles even smaller than those on the corresponding dorsal caudal rays. Free length of tenth ray 105 mm., of fourteenth 90 mm., of eighteenth 72 mm., and of twenty-first 68 mm. Margin of fin gently convex, membranes extending completely to margin, apparently little if at all emarginate. Base of ventral principal caudal 210 mm. in length.

Externally there is no clear line of demarcation between the principal and the supplementary caudal rays.

Thirty-eight supplementary caudal rays, all soft, very much compressed and flattened, and very finely articulated right down to their bases (Plate V). All the rays are spinate, the spinules basally being fairly prominent in a single series along each ray, becoming progressively smaller apically, but extending to apex, or practically so, in each case. Length of supplementary caudal, including rays, approximately 130 mm. Peduncle much compressed.

TERMINAL PORTION OF THE VERTEBRAL COLUMN.

The terminal portion of the vertebral column, chiefly of the supplementary caudal, remains. It has been severed 183 mm. in advance of the hind margin of the supplementary caudal rays. Only the extreme end, 28 mm. of the main column, remains. That portion is the end of

a slightly vertically elongated cartilaginous tube about 25 mm. vertical axis and about 20 mm. horizontal axis. The walls are composed of cartilage 2.5-3 mm. in thickness, and at this point they invest the basal portion of the lepidotrichia which run from below upwards at an angle of about 20° to the horizontal. Those from above enter at approximately the same angle.

Behind this apex the vertebral column narrows to a laterally compressed, almost solid cartilaginous structure. It contains a small fibrous core composed of numerous nerve-like threads, which appear to be the caudal prolongation of the notochordal structure. These threads are embedded in soft, spongy tissue, and extend apparently along the axis of the supplementary caudal.

On each side of the cartilage just above the lateral line, the skin appears to be thickened, forming a longitudinal ridge from the supplementary caudal forwards, to above the origin of the ventral principal caudal rays (Plates I, IV, and V). The scales along the apex of this ridge are moulded, being in transverse section very strongly arched, and, like all the caudal scales, bearing rather prominent spinules in irregular series.

The nineteenth principal ventral caudal lepidotrich (Plate XXIX) has been removed. This is 132 mm. in total length, of which 54 mm. is within the body, the inner apical 14 or 15 mm. invested by the substance of the cartilaginous notochordal sheath. This inner extremity of the lepidotrich is almost solid, the internal cavity constricting apically very rapidly to vanishing-point. This internal apex of the lepidotrich tapers gradually to a point, and this pointed apex is by cartilage firmly bound at a slight angle to the severed distal or terminal portion of a haemal "spine." This latter fragment is a lightly ossified, thin-walled, cartilage-filled cylinder, open at the apex, typically "coelacanth." It is merely a feeble perichondral ossification.

In the terminal portion of the vertebral column, at least, the lepidotrichia extend from within the substance of the chordal sheath, and are not articulated with radials as figured in reconstructions.

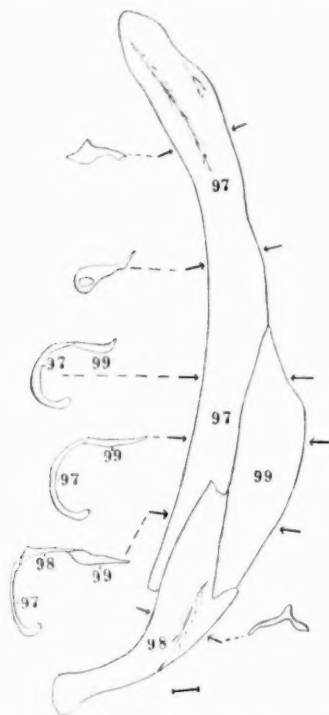
I could not distinguish any definite neural or haemal arch-like structures attached to the remaining portion of the axial sheath.

PECTORAL GIRDLE.

(Plate XXXI; text-figs. 1 and 8.)

The lower part of the pectoral girdle was fortunately not removed by the taxidermist. The remaining structure of the left side has been removed for examination. The whole structure is 270 mm. in length between the two apices. As it lies in the body it has a deep concavity in lateral view

along the major axis. From the apex the upper and lateral surfaces widen so as to be superiorly concave, and to roof over an inverted, downwardly increasing groove. That portion of the structure exposed outside the body appears to bear a coating of enamel, in part with tubercles.



TEXT-FIG. 1.—*Latimeria chalumnae* Smith. Lower unit of left component of shoulder girdle in lateral view. Cross-sections indicated by arrows with upper (lateral) surface of bone above. The line represents 1 cm. Cleithrum (97), clavicle (98), extracleithrum (99).

The clavicular "foot" of each girdle curves inwards and the inner faces articulate below the pharynx, the anterior edge being 205 mm. behind the apex of the lower jaw. The articulation was embedded in cartilage which is continued anteriorly along and above the gular articulation as a median ridge (Z) which becomes lower and smaller anteriorly (text-figs. 8 and 9).

The part of the girdle remaining is a composite, radially ossified structure, with three main ossifications (97, 98, and 99) suturally united. The

under surface of the structure is lined with cartilage to a depth of 4-5 mm. This penetrates to the apex of the fossa in the under part of the cleithrum.

CLAVICLE (98).

(Plate XXXI; text-figs. 1 and 8.)

The lowest, articulating ossification is the clavicle, of which only a small portion of one flange was exposed outside the body. The clavicle is curved, 115 mm. in length from the lower articulating face to the apex. The hind margin of the convexity lies about 35 mm. from the line joining the apices. The lower extremity of the clavicle has an articulation facet 22 mm. in width (*i.e.* running along the longitudinal axis of the fish), and is flat beneath, the upper surface being somewhat concave with slight ridges on each margin. This "foot" runs outwards and backwards, diminishing in width outwards, the ridges converging and uniting 27 mm. from the facet. This more or less truncated triangular structure forms the articulating "foot" of the clavicular system, which curves inwards from the vertical plane of the shoulder girdle. The bone at this most curved portion of the clavicle is more or less triangular in cross-section, and from 10-11 mm. in thickness. The lateral face of this structure is external, *i.e.* exposed. It curves upwards, dilating apically, and reaches up over the outer curve of the surface of the main structure. In the middle of the outer hinder margin is a deep subvertical angular notch, which lies upon the lower apex of the extracleithrum (99).

From just above the "foot" the clavicle is transversely curved, and hollow beneath, the hollow being filled with cartilage. On the top of the curve, *i.e.* on the exterior surface, is a sharp ridge which defines the exposed portion of the bone. The centre of radiation lies at the origin of the articulating "foot." The exposed surface is strongly ridged and striated with a few low tubercles near the outer trenchant margin. 65 mm. of the inner edge of the upper limb of the clavicle overlaps and articulates with the lower outer edge of the cleithrum (97), the apex of the clavicle fitting into a deep angular notch in that bone. 40 mm. of the outer margin of the clavicle overlaps and articulates with the upper inner margin of the extracleithrum (99). The clavicle thus lies upon both cleithrum (97) and extracleithrum (99), the overlapping being marginally from 2-4 mm. There is no sign of any sense-organ in this bone.

CLEITHRUM (97).

(Plate XXXI; text-fig. 1.)

The cleithrum is in some respects merely a larger, inverted, reversed edition of the clavicle (98). It has inferiorly a deep angular notch dividing

the lower apically dilated portion into two lobes, the outer much smaller than the inner. The total length of the cleithrum is 115 mm. It is strongly curved, the outer edge of the curvature being 55 mm. from the line joining the apices. From the superior apex the cleithrum is solid and heavy for 110 mm. At 75 mm. from the apex there commences in the under portion of the bone a deep and narrow fossa which at first is completely enclosed within the bone. It then emerges and expands downwards as a deep inverted channel or groove. At first the roof and sides are formed by the cleithrum alone, but at a lower point externally by the extracleithrum (99) also, while at the lowest margin, *i.e.* at the lower extremity of the cleithrum, the inner margin is formed by the cleithrum alone, the roof by the clavicle, the outer margin being clavicle plus extracleithrum.

That portion of the cleithrum which is exposed outside the body is 130 mm. in length, the edge being trenchant. The articulation between cleithrum and extracleithrum extends 70 mm. along the lower outer margin of the cleithrum. The outer lower triangular apex of the cleithrum fits into a notch between the diverging clavicle and extracleithrum.

The upper dense portion of the cleithrum is 22 mm. in width and 9 mm. in thickness at the heaviest part. The under surface is more or less smooth with a slight medio-longitudinal ridge. The upper surface has a sharp high medio-longitudinal ridge which extends almost to the apex, and which vanishes considerably below the origin of the inferior fossa. The exposed outer surface of the cleithrum is superiorly convoluted into ridges and striations. The lower exposed portion is covered with finer radiating striations. On the lower outer margin, concurrent with the upper surface of the extracleithrum, are a number of small rough tubercles.

The centre of radiation of the cleithrum appears to lie on the upper outer margin 70 mm. below the apex. The lowest margin of the cleithrum is fairly abruptly truncated, the width being 23 mm. Progressively inferiorly the cleithrum becomes thinner and more lightly ossified, so that the lowest margin of the truncated portion is scarcely more than cartilage.

There are no sensory organs in this bone.

EXTRACLEITHRUM (99).

(Plate XXXI; text-fig. 1.)

Following Moy-Thomas and Westoll (*Geol. Mag.*, 1935, vol. lxxii, No. 856, p. 454, fig. 8), the third and entirely external ossification of the shoulder-girdle is designated extracleithrum (99). It lies external to the cleithrum and the clavicle, the inner margin articulating with the outer margins of those bones as well as being overlapped by them. The extracleithrum

is 120 mm. in length, and the maximum width, which occurs about the middle of its length, is 24 mm. It is shaped somewhat like a very obtuse triangle with sides undulant, slightly convex. The upper extremity of the extracleithrum lies 130 mm. from the apex of the cleithrum. The centre of radiation lies just within the outer margin, 42 mm. from the upper apex. From this point forwards and downwards, along the major axis of the lower lobe, runs a thickened portion of the bone which shows both laterally and internally as a ridge, about 8 mm. in width, the total thickness of the bone being 8 mm. The ridge which shows laterally is more or less confluent with the upwardly curving ridge which defines the exposed portion of the clavicle. The internal ridge broadens inferiorly and forms a strong lower apex. The extracleithrum is otherwise more or less laminate, and its surface bears numerous close-set grooves, radiating the full length of the bone in all directions from the radial centre. Along the outer margin of the bone the grooves become somewhat reticulate, and within them and on the ridges lie flat rough tubercles, rather numerous, in irregular series. The outer margin of the extracleithrum is trenchant. The whole surface appears to be covered with enamel. The margin below the cleithrum is serrate for part of its length.

As has previously been indicated, the internal ossifications had been removed by the taxidermist. In so far as I have been able to judge, the fin skeleton was attached to the girdle just inside, certainly not much if at all below, the dorsal apex of the extracleithrum. Most of that bone certainly lies ventral to the point of insertion of the pectoral fin.

There are two parts of this bone which I at first took to be sensory organs. In the cancellate body are two dark oval patches, with a pore above and below. Closer examination has, however, made it almost certain that these are points at which pins (used freely by the taxidermist) had been driven through the bone in securing the opercular membrane to the body. The holes are superimposed and of such a size as to allow a small pin to slip through. The dark patch would be oily matter which has seeped into the bone from the sodden skin.

SUPRACLEITHRUM.

The supracleithrum is obviously a separate ossification in this fish, and was evidently removed when the fish was mounted. Moy-Thomas and Westoll (Geol. Mag., vol. lxxii, No. 856, October 1935, p. 454, text-fig. 8) have identified an apical ossification, forming an integral part of the cleithrum, as a supracleithrum in *Coelacanthus granulatus* Agas. There is certainly no trace of any such structure in the cleithral element of this fish.

HEAD EXTERNAL.

(Plates I, IX, X, XI, XII, XIV, and XV.)

The head bears no ordinary scales. The skin is very thick, rather leather-like (Plate XLIV), that of the opercular membrane especially being thick and wrinkled (Plate XXVI). The outer surface of the head consists partly of skin, and partly of the exposed portions of numerous surface bones.

A section of the skin from the cheek is shown in Plate XLIV. In texture it is not unlike the skin of the smaller land vertebrates.

OPERCULAR (28).

(Plates I, X, XIV, XV, XXI, XXVI, and XXVIII;
text-figs. 2, 5, and 13.)

The opercular plates are heavy and solid, and show no sign of cavernous structure. They are only slightly convex above, otherwise the surfaces are plane. The right opercular plate is 123 mm. in height and 90 mm. in maximum width. Practically the whole of the surface of this plate is exposed. Anteriorly it is fairly thick, becoming slightly thinner posteriorly. The anterior margin is broadly bevelled. The lowest point of the bone is the apex of a moderately acute angle. The hind margin is broadly rounded, above and in advance of which is a slight concavity just before the broadly convex highest point of the margin. The surface of the plate bears a few tubercles, a group occurring in the middle of the upper third of the surface. Chiefly they lie in obliquely posterior series in three main groups near the hinder lower margin of the plate, the middle group being the largest. The surface of the plate bears fine straight striae which radiate upwards, backwards, and downwards from a centre near the anterior margin. The surface is covered also with finely reticulate grooves or fine pits. The posterior margins of the plate are on a level with the investing skin.

The left opercular plate is 124 mm. in height and 88 mm. in maximum width. It is very similar in shape and structure to the right plate, but the tubercle ornamentation on the hinder margin is in a large patch, and more extensive than that on the right plate. The greatest thickness of the bone in either plate is 9 mm., and occurs at the upper anterior edge. The hinder margin is about 3 mm. in thickness. (There is a hole in the opercular made by a nail.)

Along the inner anterior margin of the (left) opercular plate is a sub-marginal ridge, thicker below than above. This is overlaid by the hollow

hyomandibular (94) and its cartilaginous extensions, which extend also 35 mm. below the lower corner of the opercular plate and form an integral part of the thick leathery opercular membrane (text-fig. 12). At the upper inner anterior corner of the opercular, the cartilaginous layer attached to the hyomandibular (94) and the opercular is about 6 mm. in thickness and covers a fairly extensive area, becoming thinner towards the hinder margin. At the upper anterior corner of the opercular beneath the skin is a rounded expansion which articulates with a facet in the lower hinder sub-dermal corner of the supratemporal (50). The lower margin of the supratemporal bears corresponding thick cartilage which envelops the articulation. This articulatory system, which is virtually a hyomandibular suspensorium, is an extremely firm structure.

SUBOPERCULAR (27).

(Plates XIV, XV, and XX.)

Immediately anterior to and overlapping the lower third of the bevelled anterior margin of the right opercular plate, is a heavily ornamented bone 60 mm. in height and 24 mm. in greatest width (Plate XIV). This bears against the opercular for 40 mm. height, 20 mm. of its hinder lower margin extending below the lowest point of the opercular plate. The exposed portion of this structure has at the apex a very acute angle, with the base approximately 24 mm. in width (Plates XIV and XX). The external surface is densely covered with irregularly radiating series of rounded-elongate tubercles closely resembling those on the anterior body scales. This structure is quite obviously merely a large vertically elongated scale (Plate XX) with the anterior portion invested in the skin partly beneath the preopercular apparatus. This probably represents an arrested metamorphosis from scale to subopercular.

On the left side of the head, which was somewhat damaged, this bone is missing, but the skin pocket which contained it is clearly visible.

INTEROPERCULAR (26).

(Plates XIV, XV, and XXI; text-fig. 5.)

Anteriorly and inferiorly to the subopercular (27) on the right side lies a small ornamented bone, the ornamented and exposed portion being 19 mm. in height and 11 mm. in maximum width. This might be regarded as a developing interopercular. This proves also to be a modified scale of the opercular membrane. An exactly similar bone occurs on the left side.

PREOPERCULAR FLAP.

(Plates XIV, XV, and XXI.)

Between the preopercular apparatus and the opercular (28), forming the basis of the connection between them, is a very thick fold of skin which is apically acutely angular (the visible portion). This sweeps down posteriorly parallel with the anterior margin of the opercular, and thence turns backwards to form a posterior, lobate, free, very thick flap strongly reminiscent of the lower preopercular flange in Teleosts.

Anteriorly this skin curves downwards and forwards, thickening to form a free infero-anterior somewhat pointed lobe with apex about 20 mm. above the origin of the mandibular canal (*e*).

In the lower surface of this subtriangular skinny flap are the interopercular (26) and the subopercular (27).

PREOPERCULAR APPARATUS.

(Plates XI, XIV, XV, and XVI; text-fig. 5.)

This consists of a vertical series of several bones, practically contiguous posteriorly, forming an almost straight posterior bony margin which is apparently free. Behind this is a vertical opening in the membrane which is possibly an hyoidean gill-slit (H). Unfortunately, the head was somewhat roughly handled during preservation, so the validity of that slit is doubtful. The general appearance of the present opening and surrounding structures incline me to the view that the species possesses that structure.

PREOPERCULAR (25).

(Plates XI, XIV, XV, and XVI; text-figs. 5 and 17.)

The lowest bone of the preopercular series is identified as the preopercular. It forms the lower angle of the preoperculum or cheek system, and in shape suggests a small hatchet with broad tapering handle, the long axis being horizontal. The surface of the bone is almost plane. The right preopercular is 78 mm. in length and its greatest height is 35 mm. The surface is excavated into pits and channels, and most of the bone is of cavernous and light structure. On the middle of the horizontal limb are a few smooth rounded tubercles set in depressions. Practically the whole of the upper surface of the bone is exposed.

The left preopercular has been removed and freed from skin. It is similar in form and ornamentation to that of the right. Its horizontal length is 75 mm. and the vertical height is 37 mm. Only a small bevelled

flange is covered by skin. The horizontal limb is laminate and fairly solid. The vertical limb is cavernous and porous. The main sensory canal runs straight through the bone from the upper inner angle, the inferior opening being at the lower margin of the origin of the horizontal limb. Several side branches run from the main channel to the vertical hind edge of the limb (text-fig. 5). The centre of radiation is at the middle of the canal, just within the inner (anterior) angle.

SQUAMOSAL (24).

(Plates XI, XIV, XV, and XVI; text-figs. 5 and 17.)

The preopercular apparatus is not symmetrical. On the left side the squamosal consists of a single bone which has been removed and freed from the skin (Plate XVI). The hind margin of this bone is very slightly concave, the lower hinder corner being somewhat pointed. The main body of the squamosal is elongate, roughly oval. On the lower third of the inner (anterior) margin is a slightly oblique, acutely angular, but apically truncated projection, which is mostly covered by the skin, the subcutaneous portion projecting forward to meet the hind upper margin of the lacrimo-jugal (48) and the lower projection of the postorbital plate (23). The upper margin of the squamosal rests against the outer lower bevelled margin of the postorbital. Height of left squamosal 66 mm., greatest width of main plate 31 mm. Total width exposed 44 mm.

The upper portion of the squamosal is practically solid, with transverse section triangular with very acute apex, the hind margin being very sharp, the anterior margin being approximately 3 mm. in thickness and broadly bevelled, the bevelling all subcutaneous. The upper margin of the bevelling is produced into two sharp points which slip below the margin of the postorbital element. The forwardly directed triangular projection is little else than a bony tube bearing the jugal canal, with posterior terminal opening on the lower margin below about the middle of the main plate. This canal also communicates superiorly and inferiorly with numerous marginal openings (text-fig. 5). The lower portion of the squamosal (*i.e.* on the main plate), where it is a projection from the tubular section, is very light and cavernous.

The upper half of the surface of the squamosal bears a more or less reticulate system of shallow pits and canals. A few scattered nodules or tubercles are present round the margin of this portion. The lower portion of this surface bears a number of deep excavations roofed by a thin membrane, which communicate with the main jugal canal (*d*). Between these the surface is pitted and striated in the same fashion as the upper portion of the bone, with only two small tubercles visible. (The plate shows a

deep excavation on the upper surface of this bone. That was made by a nail used by the taxidermist.)

On the right side the squamosal is in two parts, but there is no sign of a corresponding suture in the left squamosal. The two halves appear to be widely bevelled over the line of division, and the upper portion is much thinner than the corresponding part of the left squamosal. The upper portion is solid, apparently not at all porous (the two holes which show in the plate were caused by nails). The upper portion of the right squamosal which shows above the skin is broadly triangular, with the base subvertical posteriorly, and the apex round and blunted. Height of base 53 mm., base to apex 32 mm. The surface is covered with shallow, more or less reticulate ridges. Near the hind margin is a vertically elongated group of about a dozen widely separated small tubercles, and there are several near the upper anterior margin also. The lower portion of the bone is obviously very porous, and bears the jugal canal. It is irregularly very acutely triangular in shape, with the lower margin almost sigmoid. The hinder part of the surface bears numerous deep excavations which communicate with the jugal canal. The remainder of the surface is covered with reticulate ridges similar to those found on the upper bone. There are several small tubercles on the upper hinder angle of the bone. The squamosals have an almost plane surface, with very slight lower convexity. The centre of radiation of the left squamosal lies on the canal, just within the inner (anterior) angle.

POSTORBITAL (23).

(Plates X, XI, XII, XIV, XV, XVI, and XVII; text-figs. 5 and 17.)

The postorbital element consists of a single bone whose surface is curved more or less uniformly from the central highest area. The left postorbital has been removed and freed from skin. Its total height is 85 mm., 95 mm. along the profile of the curve. The surface of the bone is convex, the radius of average vertical curvature being approximately 60 mm. Portion exposed above the skin 30 mm. in height. The total width is 63 mm., the curvature over this line being very slight, and the portion exposed above the skin is 55 mm. in width. In shape the bone resembles a short-handled, broad-bladed hatchet with rounded cutting edge, the exposed portion of the surface being the median part of the blade. The upper rounded edge is thin, sharp, and fairly solid, thickening posteriorly to the raised central area. The remainder of the bone is virtually a housing for the infraorbital canal (*b*), and is extremely cavernous and porous. The apex of the bone is a sharp point, which is the upper origin of the main canal which runs almost straight down the bone to emerge at

the bottom of the lower projection. This lower portion of the postorbital, which is completely invested by the skin, is little else than a flattened bony tube. On the hinder margin of the upper portion of the postorbital are four large tubular openings which communicate with the main canal (text-fig. 5). There is a large dorsal pore on the top of the bone near the upper end of the canal, and three on the upper surface of the lower limb of the bone. The outer surface of the upper portion of the bone is etched out so as to give a serrated appearance. The portion of the edge of the bone which lies beneath the skin is heavily ridged and striated. In parts the surface looks as if composed of superimposed fused laminae, and the whole effect is as of elaborate sculpturing. The anterior portion of the exposed surface of the bone is excavated into pits and grooves, marginally reticulate, with one or two scattered tubercles. The middle and hinder portions of the exposed surface have deep pits and excavations roofed by membranes. The surface is also lightly pitted and grooved, and bears a moderate number of tubercles set in small pits scattered over the surface. The lower surface of the bone shows it to be composed of a solid centre from which radiate out fine tapering columnar bony structures, many of which show distal articulations resembling those of fin rays. Between these radials is stretched laminated bone which thickens inwardly. The edge of the anterior limb which lies beneath the skin, when viewed from beneath by transmitted light, shows a remarkable resemblance to a portion of a median soft fin. The centre of radiation lies on the canal slightly above the mid-line.

The right postorbital shows above the skin for the greatest height of 36 mm. and width of 57 mm. The lower margin is biconvex with a sharp excavation inwards. The hind margin is gently convex. The upper and anterior margins are somewhat irregular, having deep indentations, the inner portions of which at least are hollows in the bone, roofed by membranes. The central portion of the surface bears a number of deep excavations covered by membranes. Between these the surface of the bone is otherwise fairly smooth. Anteriorly the surface bears pits and somewhat concentric grooves. Posteriorly the surface is etched with fine grooves more or less reticulate near the margin. There is a group of scattered tubercles near the hinder angle of the bone.

LACRIMO-JUGAL (48) (SUBORBITAL).

(Plates X, XI, XII, XIV, XV, and XVI; text-figs. 5 and 16.)

The lacrimo-jugal extends on each side from below the lower narial opening to the junction of the subcutaneous portions of the postorbital and the squamosal. The lower margin is in the fold of skin which forms the

inferior margin of the cheek area. The left lacrimo-jugal has been removed and freed from skin. It is a fairly long and narrow bone 110 mm. in total length, 32 mm. in greatest depth across the posterior lobe, and tapers gradually anteriorly. The upper margin of the bone is gently concave, the lower margin almost straight anteriorly, while posteriorly it curves upwards fairly sharply convex. The bone is gently convex along the main (longitudinal) axis. In addition, the two ends have a slight anti-clockwise twist from the plane of the main surface. The whole of the lower edge of the bone is sharp and thin, the upper edge is thicker, the central portion thickest, 8 mm. in thickness. In section the bone resembles an inverted triangle with very acute apex (text-fig. 16). The upper 10 to 15 mm. of the entire length of the bone is little more than a tube for the sensory canal (text-fig. 5). The whole structure is cavernous and tubular, there being numerous openings from the main canal on the lower margin of the surface, the largest being near the hinder end. That portion of the bone which lies beneath the skin is most elaborately sculptured into grooves and ridges, and the exposed surface of the bone bears numerous deep excavations roofed by membrane. Besides those are numerous shallow pits and grooves. The anterior surface of the bone is concave (beneath the eye), and has a number of scattered tubercles around the anterior margin. The posterior surface bears a few scattered tubercles, but has obviously lost a number, the pits which had contained them being visible.

Although of a very different shape from the postorbital, the structure of the lacrimo-jugal corresponds closely in that there is a central portion from which fine rays or striae radiate out, the intervening spaces being filled by laminated bone. The radial structures do not show articulations such as are observed in the postorbital. The centre of radiation is situated on the canal midway along the bone, slightly above the mid-line.

The exposed portion of the right lacrimo-jugal is approximately 97 mm. in longitudinal length. The upper margin is more or less straight with several minor excavations. The hind margin above the skin is drawn into two sharp points. The lower margin which shows above the skin is highly contorted or sculptured. The greatest depth (28 mm.) of the exposed portion lies below the hind margin of the eye. Anteriorly the surface is gently concave, the lower surface of the bone forming a broad inferior ridge. The surface of the bone bears numerous deep pits and grooves roofed by membranes, and the remainder of the surface bears shallow pits and grooves. There are a few tubercles scattered sparsely over most of the exposed surface.

QUADRATO-JUGAL (47).

(Plates XIV, XV, and XVI; text-fig. 5.)

On the left cheek, in the area between the suborbital (48), the squamosal (24), and the preopercular (25), are three small bony studs (47) (text-fig. 5 and Plates XV and XVI). These may be the remains of an obsolescent quadrato-jugal. On the right cheek is only one such stud (Plate XIV), but its presence is significant.

CIRCUMORBITAL PLATES.

The taxidermist does not recollect having seen any such structures. That evidence is not of much significance since they would have been very light at most. The inner face of the circumorbital skin shows no trace of there having been any such sclerotic ring. It is probable that circum-orbital plates are not present in this species. There are certainly no such structures with areas exposed above the skin.

SENSORY CANAL INNERVATION IN THE CHEEK-BONES.

(Plate XVI.)

Postorbital (23).—There are seven large foramina in the lower surface of this bone below the main sensory tube. The largest is oval, about 1.5×0.5 mm., the smallest minute. There are numerous small foramina feeding the branch tubes and canals.

Squamosal (24).—The main canal in the squamosal is rather short, and there are only very small innervation foramina on the lower surface of that part of the bone. These are more numerous below the porous part of the structure, *i.e.* below the hinder outer portion.

Preopercular (25).—The inferior foramina in this bone are numerous but very small—they lie chiefly on the lower surface of the hinder limb, which is extremely porous.

Lacrimo-jugal (48).—Of these bones this bears by far the biggest foramina on the lower surface. Below the hinder portion of the canal are three more or less circular foramina, about 2 mm. in diameter, spaced about 15 mm. apart. Anteriorly are five more or less equally spaced but smaller foramina. The posterior pair are rather small, but the anterior three are larger, about 1 mm. in diameter (Plate XVI).

FRONTO-ROSTRALS.

(Plates X, XI, XII, XIV, XV, XVII, XVIII, XIX, and XXI;
text-figs. 3, 4, 5, 7, 11, 13, 15, 16, and 17.)

The fronto-rostral series of bones (1-22) covers most of the roof of the chondrocranium anterior to the intertemporals (49). There are a

number of primary dorsal pores (especially numerous anteriorly) formed by emarginations in the outer edges. Also the series of the two sides diverge from one another leaving a mesethmoidal opening of considerable extent corresponding more or less with the endochondral cavity R.

Excepting for a dorsal projection supero-lateral to the centre of ossification of the main frontal (1), all of the fronto-rostral bones are beneath the skin. This elongate-oval exposed portion of frontal (1) is firmly attached to the skin round its base and so provides a comparatively strong superficial linkage by the skin, by a similar arrangement with the intertemporals (49), over the fronto-intertemporal joint.

Most of the bones in this series are stello-laminate, none of them with centres of radiation in the wall of a sensory canal. Those which abut the canal have an inferior ridge, or ridge and groove.

Some of the anterior bones of the series are comparatively minute, and were discovered to be entities only after treatment with potash-alizarin. It is not surprising that these small anterior rostrals should be unknown or invisible in fossil remains. One or two from this large fish are mere fragments, a few millimetres in diameter.

Two bones in this series (1 and 17) rather tend to support the view that fusion of bones may secondarily occur. It is clearly shown by the nature and position of the bones in this series that they are primarily ossifications produced in relation to the sensory canals.

FRONTAL (1).

(Plates X, XI, XII, XIV, XV, XVII, XVIII, and XXI;
text-figs. 3, 5, 11, 15, 16, and 17.)

There is every reason to conclude that this frontal is a composite structure, containing three separate ossifications. It consists of two distinct limbs.

The main portion of the structure is more or less laminate, 82 mm. in total length, 35 mm. greatest breadth, and 12 mm. in greatest thickness, which occurs at the hinder lateral corner where the exposed area is situated. This plate in the main is laminate and densely ossified. The exposed portion is a more or less elongate-ovoid flat-topped projection about 23 mm. in length and 11 mm. greatest width. Its surface appears to have at most only a light covering of ganoin, is mildly striated, and bears no ornamentation.

The centre of ossification of this main lamina lies immediately beneath the inner posterior corner of the exposed area of the bone, and shows clearly on the ventral surface. The lower surface is fairly smooth. The upper surface of this main lamina is much ridged and striated radio-

longitudinally. The inner edge of the lamina is almost straight, while the lateral edge has several fairly deep emarginations into which fit the hinder parafrontal bones (11-15).

The posterior edge which forms the fronto-intertemporal joint is from 2 to 4 mm. in thickness. The inner edge, where it meets its antimeres along the mid-line of the head, is very thin and sharp. The bone thickens very gradually outwards, laterally, to about half-way across the width, when there arises rather abruptly the fairly heavy and wide inferior longitudinal ridge, whose outer lateral face supports the inner wall of the parafrontal sensory canal (*a*). A cross-section showing the structure described above appears in text-fig. 16. The dorso-lateral edge forms a great part of the roof of the parafrontal canal. The course of that canal shows clearly as a groove in the lower lateral surface of the bone (Plate XVIII).

A lateral anterior prolongation of the frontal (1) is overlapped by the hinder flange of frontal (2), and forms most of the floor of the sensory canal at that point. The parafrontals 11-15 fit into the latero-posterior emarginations, articulating superiorly with the frontal edge, laterally with one another, and inferiorly with the lower edge of the inner groove of the canal. As is described elsewhere (*q.v.* Sensory Canals), the main sensory canal in that part runs between and is carried by the frontals and the parafrontals.

The second main ossification in the frontal (1) is attached to the hinder lateral corner of the dorsal lamina, and projects slightly laterally, infero-posteriorly at an angle of about 70° from the horizontal. By contrast with the dorsal lamina this limb is somewhat cancellate in structure, although superficially of hard, more or less laminate bone. A similar infero-posterior projection from the frontal has been observed by Stensiö in fossil remains of *Axelä* and of *Wimania* (Stensiö, Triassic Fishes, Spitzbergen, 1921, pp. 65, 97, figs. 20 and 39, pls. 11, 12, 13, and 17). By virtue of the position, nature, and function of this inferior limb (1'), Stensiö's opinion that it represents an alisphenoid appears to be fully justified. As has been outlined previously, this alisphenoid (1') lies upon and is firmly bound to the antotic process of the basisphenoid (42), which rests upon, and is in turn bound to, the concave face of the metapterygoid (35) between the ascending and the antotic processes of that bone. The frontal is thus firmly connected to the pterygoid system. The upper surface of the alisphenoid is firmly attached by tissue to the lower face of the intertemporal (49), connecting that bone with the pterygoid system. This frontal composite is therefore of importance in providing rigidity by linkage to the skull.

The alisphenoid is 39 mm. in length, about 22 mm. in width, anteriorly 10 mm. in thickness, becoming lamellate posteriorly. In the middle of

the anterior third is a foramen (J) 3 mm. in diameter running forwards obliquely through the bone, through which pass presumably the ophthalmic branches of nerves V and VII.

The third ossification of this frontal composite is a small lamina which forms a posterior expansion of the postero-dorso-lateral flange of the frontal. It is possibly not an extra ossification, but may be merely the enlarged latero-dorsal flange. At any rate its outer inferior margin has expanded ventrally and become fused with the antero-supero-lateral margin of the alisphenoid so as to leave a wide canal within the bone, which lies closely dorso-lateral to the nerve foramen (J). This carries the main sensory canal from the supratemporal-infraorbital junction. This is the only portion of the parafrontal canal which runs within co-ossified structures.

By function and position it is doubtful whether this postero-lateral prolongation of the frontal is a dermo-sphenotic element, corresponding to which I can find no structure in this fish.

FRONTAL (2).

(Plates XVII, XVIII, and XXI; text-figs. 3, 5, 11, and 15.)

This second large frontal ossification is so essentially similar to the larger posterior frontal (1) in structure and function that it is designated simply as frontal also. Its junction with frontal (1) is rather different from that between the remaining bones in the series, in that its hind margin overlaps a considerable extent of the anterior portion of the frontal (1), and by interlocking of projecting points a relatively firm suture results.

The frontal (2) is laminate, of greatest length 58 mm., greatest width in posterior third 31 mm., tapers anteriorly to a width of 18 mm., and has a greatest thickness through the inferior ridge of 6 mm. The structure is laminate, with centre of radiation slightly anterior to the geometrical centre, with a small foramen in the actual centre. The inner portion of the lamina is extremely thin, and thickens laterally but little. There is an abrupt inferior longitudinal ridge with line almost on the centre of radiation. This ridge carries in its lateral face the parafrontal sensory canal (*a*), being formed almost exactly like the similar ridge described in frontal (1). The upper lateral edge projects further laterally than the lower margin of the ridge.

The lateral edge of frontal (2) has four fairly large emarginations. Into the posterior fits the hind part of parafrontal 16, while parafronto-antorbital 17 fits against the margin containing the second and third emarginations, thereby forming two large dorsal pores.

The sensory canal (*a*) in this part is carried very much as described

under frontal (1), i.e. with roof and inner wall supported by frontal (2), and floor and lateral wall by parafrontal 16 and by parafronto-antorbital 17. Anteriorly the margin of (2) articulates with the posterior margin of fronto-nasal (3).

The frontal (2) is separated by an anteriorly increasing space from its antimere. Its upper surface is comparatively smooth anteriorly, posteriorly somewhat ridged and pitted, with several fairly large excavations and foramina.

FRONTO-NASAL (3).

(Plates XVII, XIX, and XXI; text-figs. 3, 5, 7, and 11.)

This structure lies immediately anterior to frontal (2), bordered laterally by antorbitals 17 and 5, anteriorly by rostro-nasal (6), and the interior margin partly by postrostral (4).

This fronto-nasal (3) is merely a sensory canal-supporting element. It is 21 mm. in length and 14 mm. average width. It is laminate, with somewhat undulate surface. The centre of radiation coincides with the geometric centre. Inferiorly along the middle is a ridge 5 mm. in depth, which is a continuation of the inner wall of the sensory canal (*a*). As observed also in frontals 1 and 2, there are occasional deep pits and channels in this inferior ridge. There is a deep excavation in the hind part of the inferior ridge of fronto-nasal (3), which is the posterior portion of the large foramen through which the fronto-rostral commissural canal (*r*) emerges from the parafrontal canal to pass across the snout. There are several emarginations in the outline of 3 which are parts of dorsal pores.

ROSTRAL ELEMENTS (4, 7-10, 19).

Postrostral (4) (Plate XIX).—This is a small laminate bone, of shape figured, which lies between bones 3 and 7, bordered laterally by rostro-nasal 6. Its greatest length is 16 mm. and its greatest width 11 mm. Its centre of radiation lies at about the geometric centre. On the under surface is a slight laminate ridge 5 or 6 mm. in length and 3 mm. in depth. The fronto-rostral commissural canal (*r*) runs partly beneath the lateral edge of the bone.

Rostral (7) is a small laminate bone of shape shown in Plate XIX. It is 9 mm. long and not quite as broad. On the lower surface is a very slight ridge. On the upper surface are three relatively deep pits. The centre of radiation appears to lie on or about the geometrical centre. The fronto-rostral commissural canal (*r*) runs below part of the bone. In the anterior lateral face of 7 is a deep emargination into which fits the very small 7' which acts as a bridge between 7 and rostro-nasal (6), forming the anterior edge of a large dorsal pore in the canal (*r*).

Rostral (9) is a small bone about 8 mm. in length and 6-7 mm. in width, which lies anterior to 7 and 7'. It is of very fine laminate structure, somewhat arched transversely, appearing to be mainly a roofing structure to the canal (*r*). I cannot distinguish any definite centre of ossification.

Meso-rostral (8) is somewhat similar in construction to, but slightly smaller than, 7. This bone forms the anterior limit of the mesethmoidal divergence of the series, and articulates marginally with its antimeres on the mid-line. The junction between the fronto-rostral and the posterior rostral commissural canals (*r* and *h*) lies immediately anterior to 8. The upper surface of 8 has a number of small pits and is slightly concave. Inferiorly is a slight longitudinal ridge-like projection 1 mm. in height, which appears to be a centre of radiation.

Inter-rostral (8').—A small almost rectangular inter-rostral 8' lies just anterior to the capsular junction of the canals (*r* and *h*).

Rostral (10) lies anterior to 9, and is united by tissue to the lateral face of inter-rostral 8'. The surface of 10 is about 10 mm. in length and 7 mm. in width. The anterior margin is broadly convex, the posterior concave. The upper surface is somewhat convoluted, with no apparent centre of radiation. 10 bears on its lower face a large oblique inwardly directed process, 6 mm. in length and 2.5 mm. in width at the base. This inner projection appears to serve as a dividing partition where the commissural canals (*h* and *r*) diverge, i.e. the posterior rostral commissural canal (*h*) runs sharply downwards and forwards from the median capsular junction beneath the inner limb of 10.

Rostral (19) is a small elongate bone (Plate XIX) 9 mm. in length, with an inner triangular process embedded in the cranial cartilage. Its function is obscure, but it appears to form part of the dorsal pore system of the snout.

PARAFRONTALS (11-16).

(Plates XVII and XVIII; text-figs. 3 and 16.)

The bones in the series which lie along the lateral face of the frontal ("para"-frontal) are all built on the same plan, with but minor variations. Each is bilaminar, transversely U-shaped, with the lower lamina generally extending farther inwards than the upper. The inner edge of the upper lamina articulates with the outer face of an emargination in the frontal (1), the lower with the infero-lateral edge of the groove in the wall of the ridge running beneath the frontal (1). As has been explained previously, there is thus formed a fairly large canal or tube partly within the frontal and partly within the parafrontals. The parafrontals meet anteriorly and posteriorly, but in such a fashion as to form longitudinally oval apertures between each, which are the main lateral pores from the parafrontal

sensory canal (a). Most of these parafrontals have in addition some pores or foramina in their structure.

It is exceedingly difficult to find definite centres of radiation in these structures. In some cases it appears almost as if there is a centre in each lamina, but in general the appearance suggests that the centre of ossification is the bridge between the upper and the lower laminae.

Parafrontal 11 consists of two rhomboidal laminae joined so that the upper is set more laterally than the lower. Both laminae have a fairly plain surface. In addition to the connecting ridge of bone there is a slight stirrup-like projection connecting the upper with the lower lamina posteriorly which forms a small separate lateral pore.

Parafrontal 12 is of slightly different structure, the lower lamina being very thin and flat, with a foramen near the hind margin. The upper flange is small and comparatively thick, ridged and convoluted. There is a small lateral foramen within the bridge joining the upper and the lower laminae.

Parafrontal 13 is very similar in structure to 12, with a foramen in the comparatively large thin lower lamina. The upper flange is thick, ridged and convoluted, much smaller than the lower. There is only a minute foramen through the bone which connects the upper and lower segments.

Parafrontal 14 has smaller laminae than the preceding, the lower extending not much farther inwards than the upper. The canal at this point is borne chiefly by the frontal (1), more than at any other point along that bone. There is only a minute lateral foramen through the bridge connecting the upper and lower segments.

Parafrontal 15 differs somewhat abruptly from the preceding. The upper lamina is if anything greater than the lower, both are rather thick and rugged, the whole bone being much convoluted, pitted, and channelled. The bridge uniting the upper and lower flanges is comparatively narrow. The relatively deep excavations between the flanges at each end form rather large lateral primary pores from the canal. There are numerous foramina on all parts of the bone.

Parafrontal 16 is the greatest in this series, being 27 mm. in total length. It is a fairly robust structure, much convoluted. The upper and the lower laminae have thin inner margins thickening fairly rapidly laterally. There is a longitudinal inferior ridge beneath the lower flange or lamina. The bridge connecting the two flanges is only 4 mm. in length, and the lower flange is much longer than the upper. There are several oblique foramina in the lower flange, possibly connected with the innervation of the canal.

The anterior portion of 16 fits by the projecting processes into corre-

sponding recesses of, and interlocks with, the hinder portion of parafronto-antorbital (17), so as to produce a rigid union. When so united, 16 has all the appearance of being a part of the complex 17. The parafrontals 11-14 do not interlock in this fashion. They are held in position more by their articulation within the emarginations in the lateral edge of frontal (1), so that inter-support is not so necessary as more anteriorly, where the parafrontals merely lie against the outer face of the frontal (2). There is slight interlocking between 15 and 16. This transition from loose articulation to anterior firm suturing is significant in relation to the nature of the parafronto-antorbital 17.

PARAFRONTO-ANTORBITAL (17).

(Plates XVII and XVIII; text-figs. 3 and 5.)

There is very little doubt that 17 is a composite structure, since it shows clear indications of containing at least four co-ossified parafrontal elements, with a probably still later addition in the form of an antorbital expansion. The structure is 40 mm. in length. The inner portion is bilaminate, with flange above and below, and forms the lateral wall of the parafrontal canal (*a*). From this open four large pores, the posterior lateral, the anterior by transition becoming dorsal. Anteriorly there is a laminate lateral flange proceeding chiefly from the anterior two parafrontal elements, with an acute projection at the anterior lateral corner. There is a distinct centre of ossification near the mid-point of the inner margin of this antorbital flange.

The anterior portion of this structure 17 is almost an enantiomorph of the anterior part of frontal (2). The structure of this parafronto-antorbital (17) is of great interest in throwing some light upon the controversy about the possibility or otherwise of the fusion of ossification elements.

ROSTRAL BONES 20, 21, and 22.

(Plate XIX; text-fig. 4.)

These bones lie almost vertical in the rostrum. There are three elements arranged as shown in text-fig. 4. There is a distant gap between the fronto-rostrals and these three bones. The latter are very light structures which demonstrably can have no tooth-supporting function, and cannot be regarded in any light as "premaxillae." They are probably the remains of a more primitive continuous fronto-rostral series of bone-elements.

The inner-rostral 20 is laminate, with a roughly square body and two lateral acute projections, the upper greater, forming a concave lateral edge. The "body" is about 6 mm. square. On the lower face is a small

lamine projection which appears to mark the centre of ossification. The rostral commissural canal (*g*) apparently runs between 20 and 21, as shown in text-fig. 4.

The mid-rostral 21 is a slender bone which has fallen into two parts. I cannot be certain whether the fracture is accidental or whether two bones are actually present. As it occurred after potash-alizarin treatment, and the faces of the junction are unstained, it is likely that it is a fracture and not an articulation.

The upper lateral limb of this bone lies over the rostral narial aperture (A). The rostral commissural canal (*g*) passes below a small flange in the foot of 21.

Outer rostral 22 is a small semicolumnar bone set obliquely lateral to the rostral tube (A), so as to form with 21 a bony ring support for that channel. This bone has also split into two parts, almost certainly not a suture.

The rostral dental plates (90) are supported almost entirely by the extremely thick and strong skin of the rostrum. The slight rostral skeleton can hardly add much to the strength of that part.

NASO-ANTORBITAL (5).

(Plates XVII and XIX; text-figs. 3, 5, and 7.)

This bone is structurally somewhat difficult to interpret. It represents almost a transitional form between the anterior portion of the composite 17 and the larger canal ossification such as frontal (2). There are indications that it contains two fused parafrontal elements and a lateral antorbital ossification, but this is not so obviously shown as in the case of bone 17.

This antorbital is 22 mm. in length, 19 mm. greatest width, and transversely fairly convex. It is laminate, somewhat ovoid, with the hinder lateral margin expanded and somewhat serrate. The upper surface is uneven, with moderate grooves and ridges. Two large pores open from the canal on the inner part of the surface.

Inferiorly is a longitudinal ridge which forms the lateral wall of that part of the parafrontal canal (*a*) where it trifurcates, inwardly into canal (*r*) outwardly and laterally to meet the infraorbital canal (*b*), and anteriorly to run around the inner face of the naso-rostral 18.

The apex of 5 rests upon the front flange on the hinder edge of rostronasal 18, and the inferior ridge is supported by a long postero-inferior process of that same bone (*q.v.*). 5 articulates with bones 17, 3, 6, and 18.

The centre of ossification is not obvious, but it appears to lie just lateral from, and anterior to, the large inner posterior pore.

ROSTRO-NASAL (6).

(Plates XVII, XIX, and XXI; text-figs. 3, 5, and 11.)

This bone lies at the centre of the rostro-nasal system. Its outline is much excavated, forming part of the numerous dorsal pores which are present in this area. 6 is an important bone in its relation to the sensory canals, and it articulates with bones 3, 4, 5, 7, and 18. The upper surface is slightly ridged and pitted, and gently convex. The shape is difficult to describe; the bone is shown in Plate XIX. Its greatest length is 16 mm. and its greatest width is 14 mm. The superficial portion is laminate.

Posteriorly is an apically dilated limb which articulates with fronto-nasal (3). Beneath the base of this limb is an inferior, rather acute process 8 mm. in length and about 4 mm. across the base, which projects backwards and downwards. This forms the anterior margin of the large pore in the inner wall of the parafrontal canal through which the commissural canal (*r*) issues.

The parafrontal canal runs beneath the hinder lateral edge of 6, continuing down beneath that bone round the inner face of naso-rostral 18. The fronto-rostral commissural canal (*r*) runs beneath the inner face of 6.

The lower surface of 6 is deeply concave anterior to the inferior process, with a pit at the foot of that process in which appears to lie the centre of ossification. Here again ossification has originated next to a canal system, has proceeded above and below the canal, and has also produced a laminate contra-expansion.

INNERVATION OF THE PARAFRONTAL CANAL SYSTEM.

In the antero-lateral flange of the alisphenoid (1'), which underlies the canal, are several minute, possibly innervation, foramina. Parafrontal 16 also possesses several oblique foramina (*q.v.*). Otherwise there are no indications that the innervation of the parafrontal canal occurs by transmission through any part of the ossified walls. In some parts, *e.g.* the hind lower edge of the infra-frontal (1) ridge, there is a slight groove leading to the canal from the foramen (J), indicating direct supply from the main trunk of the nerve.

As described under Sensory Canals, the parafrontal canal proper is nowhere entirely encased in bone. The floor of the canal is posteriorly partly cartilage, increasingly so anteriorly. The innervation is doubtless through the cartilaginous floor.

LATERAL ROSTRO-NASAL (18).

(Plates XVII, XIX, and XXI; text-figs. 3, 4, 5, 7, and 11.)

This bone is situated at the side of the rostrum, its base resting in a notch on the lower portion of the outer face of the ectethmoid (38), its lateral limb resting against the upper part of the face of the columnar process of that bone. The lateral limb anastomoses with the anterior end of the suborbital (48). The upper limb of the rostro-nasal is overlapped by the lower lobe of the naso-antorbital (5), and slightly below and inwards by rostro-nasal (6) (text-fig. 3). The body of the bone forms the anterior wall of the olfactory capsule (E) (Plate XXI).

The shape of the bone (18) is difficult to describe, but it is figured in Plate XIX. The ossification has very obviously been developed in relation with the sensory canal system. Canals run round the margin and within the bone for at least four-fifths of its periphery. The centre of radiation lies near the inner margin of the main body of the bone.

In structure the body of the bone is light, but firmly ossified. The more distal parts are laminated and densely ossified.

The lateral limb is merely a tube with two elongate-oval apertures facing upwards and outwards. The inner margin of the bone is excavated into a deep groove with a uniform flange behind, and with a doubly emarginate flange anteriorly. Towards the lower part of the inner margin the two flanges fuse distally to form a short tube which opens into a shallow groove on the lower face and ends on the slightly dilated "foot" of the structure.

On the inner face of the lateral tubular limb is developed an elliptical facet for articulation with part of the columnar process of the ectethmoid (38) (the corresponding facet on that bone (38) may be seen, Plate XXII).

This rostro-nasal is an important bone in the sensory canal system of the head. Over the upper hinder flange, turning outwards (lateral), is the junction between the parafrontal and the infraorbital canals (*a* and *b*). This junction is continuous with the canal running round the inner margin of 18 (text-fig. 3). This rostral branch of the parafrontal canal receives the two rostral commissural canals (*g* and *h*) (text-figs. 3, 4, and 5).

On the inner face of the bone along the course of the canal system are several small foramina, possibly for innervation. There are also several larger foramina in the back of the body of the bone (which is porous), which appear to communicate through the bone with the base of the trough of the canal groove which runs round the upper and inner edge of the bone. There are also numerous small foramina on the postero-dorsal slope of the lateral tubular arm of the bone which probably are connected with the innervation system.

INTERTEMPORALS (49).

(Plates X, XI, XII, XIV, XV, XVII, XXI, and XXVIII;
text-figs. 2, 5, 11, 13, 17, and 18.)

The intertemporals form the chief portion of the bony roof of the cranium. They appear to be more firmly united along the median suture than are the frontals, and are much heavier bones. There are no tubercles on the exposed surface of the intertemporals, though there are several pits which might have contained them. The portion exposed above the skin is approximately half of the total superficial area, and lies latero-anteriorly. This portion of the bone is divided into three main areas by grooves, a small, fairly deeply excavated groove demarcating a small area at the infero-anterior corner. The main groove is paraboloid and defines the hind limb of the exposed surface. Medially within the anterior part of this section is a short longitudinal groove. The base of these grooves consists partly of membrane, which is a roof to sensory tubules within the bone. The surface is generally striated and convoluted, with centre of radiation approximately at the nose of the paraboloid groove. The hinder upper margin of the exposed surface is deeply concave. On the inner edge of the exposed surface is a rounded projection. The greatest length of the exposed portion of the left intertemporal is 59 mm. and width 44 mm.; length of exposed portion of right intertemporal 58 mm., greatest width 44 mm.; length of the surface of the whole intertemporal 77 mm. and greatest breadth 67 mm.

The anterior edge of the intertemporal does not articulate above with the hind margin of the frontal (1), but they meet below, the system comprising the characteristic fronto-intertemporal joint (*q.v.*). A small projection from the anterior edge of the intertemporal almost touches the outer surface of the alisphenoid. Time and circumstances have not permitted of a dissection of this region, but the general character of the intertemporal has been determined. Along the medio-sutural line the intertemporals are radio-laminate. About 20 mm. from the inner margin there is an abrupt, ventrally directed longitudinal ridge. At the anterior end of the ridge the bone is 8 mm. in depth, but increases posteriorly as this ridge becomes higher. The ridge is trenchant, and forms the upper lateral support for the chondrocranium in that region. About 65 mm. from the anterior margin of the intertemporal the cartilaginous floor of the superior fossa temporalis joins that lining, the lower surface of the intertemporal forming the posteriorly sloping posterior surface of the cranial cavity. The apex of the fossa temporalis is formed by a conical fossa in the intertemporal itself.

The main sensory canal (f) runs in a tube through the bone along the lower lateral edge of the intertemporal, and ends anteriorly 20 mm. behind its anterior outer angle, where the under surface of the bone acts merely as a roof for the canal. Just in advance of the anterior end of the main tubule, 15 mm. from the anterior margin of the intertemporal, is a dorsal branch of the sensory canal which appears to run almost 20 mm. dorso-medially (text-fig. 2). It must branch in all directions, since the upper portion of the bone is extremely porous, and side tubules from the dorsal branch are visible, and may be traced all round the edge of the exposed portion of the bone.

SUPRATEMPORALS (50).

(Plates X, XI, XII, XIV, XV, XXI, XXVI, and XXVIII;
text-figs. 2, 5, 11, and 13.)

The supratemporals lie immediately posterior to the intertemporals (49). The anterior face articulates with and is closely joined with the latero-posterior face of the intertemporal beneath the skin. The two bones are definitely not fused, but time and circumstances have not permitted me to separate them. The exposed portion of the left supratemporal is 40 mm. in length, 20 mm. in width, broadly hastate with anterior apex. The surface bears a number of pits and short grooves. The right supratemporal is 35 mm. in length and 22 mm. in width, somewhat similar in shape to the left but with more dermal invasion of the surface, the outer margin being somewhat irregular. Considerably less than half of the dorsal surface of the left supratemporal is exposed above the skin; the unexposed portion lies chiefly postero-dorsally.

The total length of the supratemporal is 70 mm. and its greatest width 38 mm. The hinder limb beneath the skin is deeply concave, and forms the lateral surface of the dorsal fossa temporalis. The lower hinder corner of the supratemporal is expanded ventrally beneath the skin. The slightly oblique hinder face bears a moderate facet for the articulation of the antero-superior opercular process, the whole being enveloped in the hyomandibular cartilage. The anterior portion of this inferior projection is produced downwards, forwards, and slightly inwards into an elongate lamina (50'), 41 mm. in length, which articulates by overlapping with the upper outer hinder face of the prootic (93) beneath the capsular ossicle (92) (text-fig. 11 and Plate XXVIII). A smaller, inwardly directed horizontal process from this downward process 50' articulates with an outwardly projecting similar structure from the inner lower ridge from the intertemporal (49).

POSTSPIRACULAR (51).

(Plates X, XI, XII, XIV, XV, XXI, and XXXII;
text-figs. 2, 5, and 11.)

This structure lies at the posterior extent of the postspiracular groove (T) between the intertemporal-supratemporal suture and the upper hinder margin of the postorbital (23).

That of the left side has been removed and, like the subopercular (27) and the interopercular (26), proves to be merely a modified scale. The exposed surface is roughly oval, 18 mm. in length and 8 mm. in height. This bears dorsal and ventral dermal flanges set at almost right angles to the exposed surface. The upper flange is about 3 mm. and the lower 5 mm. in height, both being rather thin with sharp edges. These flanges continue beneath the skin anteriorly, diverging somewhat, and are connected by a dermal expansion originating below the anterior margin of the exposed surface. This antero-inferior expansion is deeply emarginate anteriorly, and the degree of ossification diminishes rapidly towards the margin, which is cartilaginous.

The whole structure from above resembles a rather elongate arrow-head. In transverse cross-section the ossicle is very strongly arched. The whole structure resembles a trough, of which the exposed surface is the bottom and the dermal flanges the sides. The hollow portion is filled with very oily spongy tissue. On the exposed surface are a number of rounded tubercles, between which the surface appears to bear a thin coating of ganoin.

The postspiracular of the right side is somewhat larger (Plate XIV), but obviously of similar structure.

EXTRASCAPULARS (55-59).

(Plate XXX; text-figs. 2 and 5.)

The extrascapulars are in this fish small tubular ossifications, the outer pair indeed being merely roofing structures for the occipital sensory canal (*f*). They form an undulating chain across the occiput with a central composite inter-extrascapular (55). The whole system of nine elements lies immediately beneath the skin, being held firmly in position by a stout periosteal membrane in which the tube is continued between the individual structures. The mouths of the tubes are separated one from the other by a space of several millimetres.

There is a medial composite inter-extrascapular (55), and on each side four small units, the first, second, third, and outer extrascapular (59). This system is possibly a remainder by reduction of dorsal ossifications,

for these tubular bones may easily have originated by modification of tubules such as those carried by the first few lateral-line scales. The tubules in 55, 56, and 57 resemble the tubules of the anterior lateral-line scales, but are larger. There is differentiation between these bones and the other canal-bearing bones of the head, in that none shows any centre of radiation. On the occiput, adjacent to the canal, is a small bony stud (95) in the skin, which may be the remains of the superficial occipital ossifications. It resembles those studs in the quadrato-jugal region (47).

INTER-EXTRASCAPULAR (55).

This bone lies immediately beneath the skin on the mid-line of the occiput. It consists of a more or less capsular central portion from which radiate out numerous tubules. On each side is the main anterior limb anastomosing with the first extrascapular (56). Medio-anteriorly on the capsule is a large pore. Posteriorly to that part in contact with the under surface of the skin radiate out four main tubes and several minor tubules. The dorsal surface of the capsule contains numerous small pores leading to the skin.

The main capsule is about 14 mm. in diameter and 8 mm. in thickness. The apices of the main anterior limbs are 24 mm. apart internally. The structure is laminate with no obvious centre of radiation.

FIRST EXTRASCAPULAR (56).

This extrascapular anastomoses with the lateral limb of 55. It is a tubular structure, fairly simple, of laminate bone, somewhat convoluted, with the ends moulded for each anastomosis. Its length is 18 mm., outer diameter 6 mm., inner 3 mm. In the dorsal surface are relatively large foramina, while on the ventral surface, near the anterior margin at the centre of the bone, are three forwardly directed spiniform processes. Posteriorly there are a number of pits.

There are three side branches to the main canal in this bone, two anteriorly and one posteriorly. There is no obvious centre of radiation.

SECOND EXTRASCAPULAR (57).

This is a tubular structure of somewhat irregular shape, 15 mm. in length, outer diameter about 5 mm. and inner about 3 mm. The ends are to some extent moulded by dilation to allow for the bending of the canal at this point. The dorsal surface contains numerous pits and excavations, while midway along the anterior side is an antero-inferior spiniform process. There is no obvious centre of radiation.

THIRD EXTRASCAPULAR (58).

This lies between the outer extrascapular (59) and the second extrascapular (57). It is a laminate bone curled about the long axis for about four-fifths of the extent required for the edges to meet and form a tube. It is almost a tube, only a portion of the floor being open. Its length is 13 mm. and the diameter of curvature about 5 mm. The bone is of the same type as 59, merely curled to a greater extent, and contains foramina and internal excavations. It forms the roof and sides of the canal. There is no obvious centre of radiation.

OUTER EXTRASCAPULAR (59).

This is merely a more or less rectangular laminate ossification with rounded corners, and with the long edges curled slightly downwards. It forms the roof of the canal over the depression containing the end of the canal in the upper hinder surface of the supratemporal (50).

There are numerous foramina in the bone, and a spiniform dorsal process near the mid-point of the anterior edge. Its anterior end is close to the postero-lateral end of the third extrascapular (58). Its length is 14 mm., width 9 mm., the bone being at most 1 mm. in thickness. There is no obvious centre of radiation.

SENSORY SYSTEM.

(Plates XVII and XXV; text-figs. 2, 3, 4, 5, 7, 9, 15, 16, 17, and 18.)

In the main the sensory canal system in the Coelacanthid head appears to differ but little between the genera. The present specimen indicates that most of the recent authoritative reconstructions have probably been very close to the truth.

In the present specimen the courses of the main canals have generally been very plainly shown by encasing bones. To some extent the actual shape and size of the internal cavities have been difficult to determine exactly, since that would have meant opening the bones, which I could not contemplate. Some portions of the canals have been exceedingly difficult to determine, since the tissues beneath the skin had been torn and scraped away. In the following description any doubtful points are clearly indicated.

Isolated pit-organs are not obvious either on the head or the body. They would in any case be difficult to identify, since everything had been soaked in oil, and later heavily varnished (though most of the latter has been removed by washing with chloroform subsequently). I cannot find definite pit-lines such as have been stated to have been found in several

extinct forms. The sensory system in the dermal bones of this specimen is very complex, but practically every part of it is directly connected with the main canal system. Almost the whole of each bone is porous and channelled within, presumably everywhere connected with the main canal. Innervation foramina are generally visible beneath the porous area as well as below the main canals. Above those parts connected with the sensory canals the surfaces of the bones are much sulcated, the bottom of the grooves being membranous. On the cheek-bones all this may clearly be seen in Plate XVI, and the approximate degree of excavation within the bones is shown in text-fig. 5.

The angular and splenial have no definite pit-line, though in each there are several sensory grooves and large pits; in the former these run along the line of the canal, almost regularly spaced. The hinder limb of the mandibular canal ends in an extensive membrane-roofed groove. As has previously been stated, the gulars possess isolated sensory grooves and large pits.

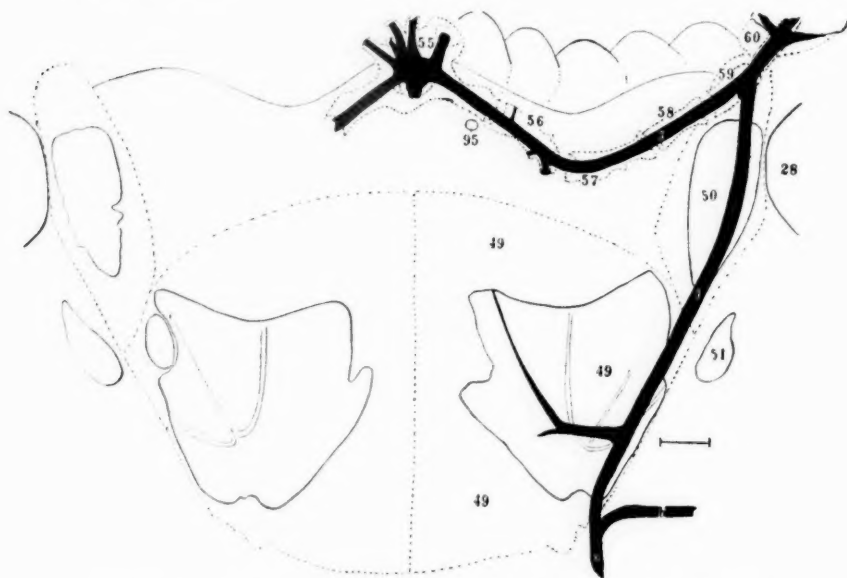
It is possible that the canal system of *Latimeria* represents the general plan for all Coelacanthids. Variations shown for certain genera and species are probably due to distortion of the structure.

OCCIPITAL REGION.

The main canal system of the occipital region has been determined in detail. The lateral line from the trunk joins the head through the tubule of the first lateral-line scale (60) (text-figs. 2, 5, and 17; Plates X, XV, XXI, and XXX), whose anterior opening lies over the end of the supratemporal (50). At this point, about 6 mm. from the hind end of the supratemporal, is a depression into the bottom of which the tube through the supratemporal runs obliquely. This depression is covered partly from behind by the anterior opening of the first lateral-line scale, anteriorly by the hind margin of the convex, laminate outer extrascapular (59), whose hind margin articulates with the upper anterior portion of the tube of the first lateral-line scale. The canal rising from the supratemporal thus divides into a posterior branch which is the lateral line of the trunk, and an anterior which is the supratemporal commissural canal (*t*) of the occipital region. More properly the supratemporal canal (*f*) might be regarded as an infero-anterior offshoot of the canal of the lateral line which is continuous across the occiput.

From this junction on the supratemporal, the supratemporal commissural canal (*t*) runs almost parallel with, and just in advance of, the anterior margin of the scaling on the nape. The canal runs upwards and forwards, first beneath the laminate outer extrascapular (59), then beneath

the third extrascapular (58), continuing forwards through the second extrascapular (57). Towards the end of the tube in that bone (57) the canal turns to a transverse course, and thence upwards but obliquely backwards through the first extrascapular (56), then through the left lateral limb of the inter-extrascapular (55), where it meets its fellow from the opposite side.



TEXT-FIG. 2.—*Latimeria chalumnae* Smith. Sensory canal system of occipital region. Canals in black. Bone surface above skin with uninterrupted, below skin with interrupted, outline. The line represents 1 cm. For explanation see Folder-page I at end.

Only in the first extrascapular (56) are there any branches from the main canal. It is possible that branches may occur between the ends of the comparatively widely separated extrascapulars, but I was unable to examine the under surface of the skin in that part of the head to determine this. The inter-extrascapular (55) is radio-tubulate with five posterior and one large anterior branches.

Innervation.—There is little to assist in determining the mode of innervation of this canal. Laterally, where the canal has a roof only, this is obviously transmitted through the soft floor. Bones 56 and 57 do not appear to have any even minute foramina in the ventral surface, though there are a few on the posterior face of each. There are none in the floor

of the capsule of the inter-extrascapular but a number on the anterior slope of the capsule above, sheltered by a superior flange below the main anterior branch of the canal. These may be the innervation foramina. It is most likely that the main innervation occurs between the bones of the system.

SUPRATEMPORAL CANAL (*f*).

(Text-figs. 2, 5, 17, and 18.)

From the posterior dorso-lateral end on the supratemporal (50) the tube passes downwards very obliquely through that bone, running towards the lateral edge. It passes into the intertemporal (49), in which it apparently runs close to the lower lateral margin. About 30 mm. behind the front margin of the intertemporal is the anterior aperture of the tube. The canal runs thence forwards roofed by the lateral ridge of the intertemporal.

There are indications of side tubules and branches in the supratemporal although that bone is comparatively solid. The intertemporal is, superficially at least, apparently cancellate or porous in structure, and there are doubtless very numerous small branches from the main canal. There is one large dorsal branch in the intertemporal, which originates in the roof of the groove above the anterior portion of the main canal. It runs almost transversely upwards near the surface of the intertemporal (49), as shown in text-fig. 2. Only one branch from that dorsal section can be traced with certainty. It runs upwards and backwards, ending at the upper hind margin of the exposed portion of the bone as a membrane-covered depression. Since numerous other similar depressions are present round that margin, there are doubtless very many branches from the main canal as well as from the main dorsal branch.

PARAFRONTAL CANAL (*a*).

(Text-figs. 2, 3, 5, 7, and 16.)

From beneath the roof of the intertemporal lateral edge the main canal passes forwards and downwards to run through the upper outer foramen above the "alisphenoid" (1'), i.e. the hinder limb of the frontal (1), below but lateral to the fronto-intertemporal joint. It emerges from the foramen of the alisphenoid beneath the superior lateral flange of the frontal (1), and runs along the lateral margin of that bone.

The nature of the canal in this part is more "parafrontal" than supra-orbital. In no part in advance of the alisphenoidal foramen is it carried by a bone-encased tube, but travels between more or less articulating bones. As is mentioned elsewhere, if bone fusion is accepted, the foramen

along the "alisphenoid" (1') has been formed by fusion of the lateral margins of the alisphenoid and of a parafrontal element (likely not a dermosphenotic by function), after both had fused internally with the lateral margin of the frontal.

Along the lateral edge of the frontal (1) the canal is formed as follows: the inner wall entirely, and the floor only partly by the frontal (see Plate XVIII); the floor posteriorly only partly by the inner lower flanges of the parafrontals 11-16; the roof chiefly by the dorso-lateral flange of the frontal (1), partly by the inner superior flange of the parafrontals; the lateral wall by the lateral rounded portion of the transversely U-shaped parafrontals. The system is extremely open, the parafrontal bones being so formed that there is a large pore opening laterally between each pair. The first large pore is formed between the hind outer margin of the first parafrontal (11) and a gap in the outer edge of the foramen above the "alisphenoid," where it emerges laterally and anteriorly. Along the edge of the frontal (1), behind its articulation with frontal (2), there are so formed six large lateral pores. The first (posterior) pore, behind the first parafrontal (11), appears to have a posterior expansion along the edge of the frontal (1).

The canal widens somewhat anteriorly and continues undivided along the lateral edge of frontal (2), roofed partly as before by the dorso-lateral flange of that bone. Its outer margin and the lateral part of the floor are formed by parafrontals 16 and the composite 17. The series of lateral pores is continued, the seventh large pore being between the anterior margin of 16 and the posterior margin of 17. The following five pores in that series gradually change from lateral to dorsal over the surface of the fronto-antorbital (17), the last being on the surface of bone 5. In addition to these latero-dorsal pores there now commences a series of anteriorly increasing pores in the roof of the canal. The first is formed between the lateral margin of frontal (2) and the inner margin of parafrontal 16, the second and third between frontal (2) and the dorso-inner flange of parafrontal 17. Beyond this third pore the anterior margins of 2 and 17 diverge and the fronto-nasal (3) comes between them. The fourth large pore is formed between the three bones mentioned (2, 3, and 17).

It is characteristic of the parafrontal canal that it becomes somewhat wider anteriorly, and the bone encasement less, chiefly in the floor. Between bones 3 and 5 there is scarcely any bony support for the canal below.

The canal continues between the outer margin of 3 and the inner margin of the naso-antorbital (5), with the fifth large dorsal pore formed by emarginations in their contiguous edges. Anterior to the articulation between 17 and 5 on the lower third of the latter, the parafrontal canal (*a*)

divides, the outer or lateral portion passing beneath the inner margin of 5, thence over the hinder dorsal flange of the latero-rostro-nasal (18), turning sharply latero-posteriorly through the tube in the postero-lateral limb of 18, to join the infraorbital canal (*b*) at its exit from the anterior end of the suborbital (48). At the lower corner of 5 there is another bifurcation, the inner limb passing round the inner furrowed edge of 18, where the posterior rostral commissural (*h*) joins, thence to the lowest anterior point of 18, where the rostral commissural (*g*) ends.

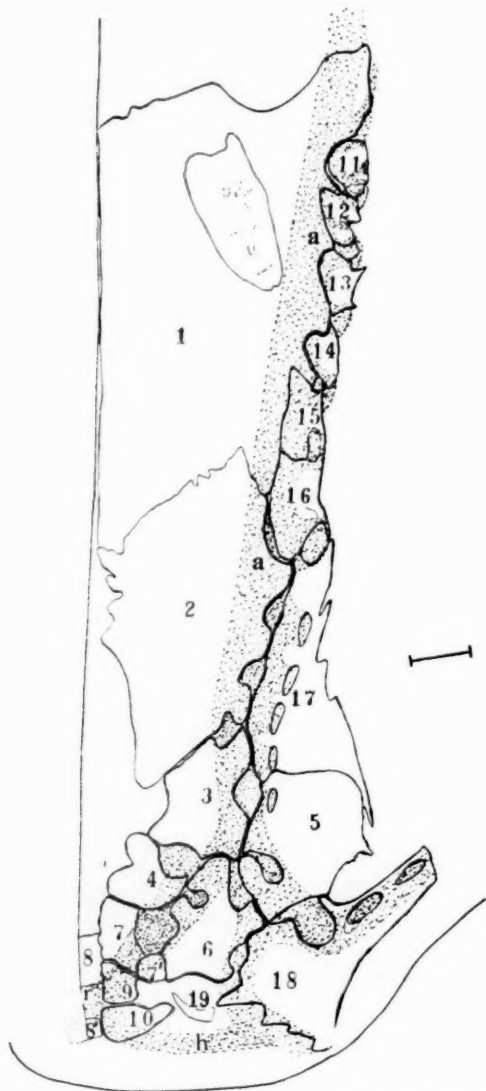
The parafrontal canal has in all 17 primary pores—10 latero-parafrontal, 3 dorso-frontal, and 4 ethmo-rostral. The innervation of this canal has been discussed elsewhere (*q.v.*).

ROSTRAL COMMISSURAL CANALS (*r*, *h*, and *g*).

(Text-figs. 3, 4, 5, and 15.)

The condition of the specimen has made it extremely difficult to determine exactly the course of each of these three canals. The skin on the snout has set to an almost metallic hardness and the tissues within have shrunk with some degree of decomposition, so that the tracing of the course of the anterior rostral commissural canal (*g*) with absolute certainty has proved almost impossible. The course of neither (*g*) nor (*h*) is defined by bones only, but passes through subdermal tissue. Only in the case of the fronto-rostral commissural canal (*r*) has the course been determined beyond doubt, since it is bordered by inferior processes or flanges of the rostro-nasal series of bones.

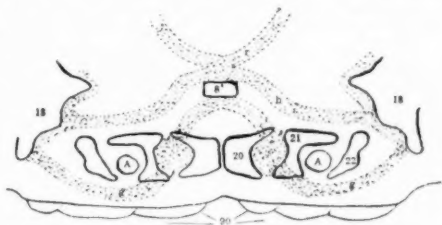
The Fronto-rostral Commissural Canal (r).—By the sutural union of the recessed inferior longitudinal processes of fronto-nasal (3) and rostro-nasal (6) is formed a large foramen which is the junction between the parafrontal canal (*a*) and the fronto-rostral commissural canal (*r*). This latter is fairly broad, but not so great as the parafrontal canal (*a*). It runs forwards and inwards, at first beneath the hinder inner portion of rostro-nasal (6), partly beneath rostrals 7, 7', and 9, and finally meets its fellow on the mid-line as a purely dermal canal immediately anterior to the meso-rostral (8). At its junction it also unites with the posterior rostral commissural canal (*h*), forming a central cavity which lies between meso-rostral (8) and inter-rostral (8'), from which on each side (*r*) runs upwards and backwards and (*h*) forwards and downwards. Between the junction with the parafrontal canal (*a*) and the small median capsular junction there are three large pores above this fronto-rostral commissural canal (*r*). The first lies above and inwards from rostro-nasal (6), being bordered by that bone and by the bones 3 and 4. The second, anterior to the first, is small, and lies almost wholly within the surface of 6. The



TEXT-FIG. 3.—*Latimeria chalumnae* Smith. Dorsal view of fronto-rostral series of bones on left side. Sensory canals shown by dotted areas (see Plate XVII). The line represents 1 cm. For explanation see Folder-page I at end.

anterior and largest pore is bordered by 4, 6, 7', and 7. I am inclined to think that the large open area between the fronto-rostral series on the mesethmoidal area (above the cavity R) may be connected with this commissural canal. Also anterior to bones 6 and 7', posterior to 10 and 19 and between 9 and 18 (see text-fig. 3), are two large dorsal pores bordered partly by tissue which may possibly connect the canal (r) with the canal running round the inner face of the latero-rostro-nasal (18). Those two openings suggest that they are sensory canal pores.

Posterior Rostral Commissural Canal (h).—From the central capsular junction with commissural canal (r), the canal (h) runs sharply downwards and forwards, beneath the inner portion of rostral 10, over inter-rostral 8' to above rostral bone 21, whence it appears to turn sharply, latero-horizontally to join the canal on the inner face of bone 18 (see text-figs. 3 and 4).



TEXT-FIG. 4.—*Latimeria chalumnae* Smith. Sensory canals of rostrum shown by dotted courses. About natural size. For explanation see Folder-page I at end.

Rostral Commissural Canal (g).—The only portion of this canal that can

be determined with any certainty is the median portion immediately anterior to inter-rostral 8'. The canal turns sharply forwards and downwards with apparently a large dorsal pore between rostrals 20 and 21 (this shows externally on each side as a large depression in the shrunken skin internal to the rostral narial opening (A) (see Plates X, XI, and XII)). In so far as I can determine this canal now passes forwards, turning laterally over the foot of rostral 21, thence upwards beneath rostral 22 to join the main canal system at the inner side of the foot of latero-rostro-nasal (18). It is possible that the commissural canal (g) joins into the posterior rostral commissural canal (h) above the rostral 21. The nature of the skin in that part led me to believe that the commissural canal (g) ran principally that way. More careful study of that part appears to confirm the canal system here outlined and as shown in text-figs. 3 and 4.

In my opinion it is not unlikely that almost the whole of the surface of the rostrum, in advance of rostro-nasals 6 and between latero-rostro-nasals 18, is directly connected with the sensory canals. Commissurals (g) and (h) represent merely the main channels in those parts, and are probably interconnected by numerous smaller channels.

and the infraorbital canals had been scraped and all loose tissue torn away. (This part had been damaged and sewn up rather coarsely.) The precise point at which the infraorbital canal joins the superior canal could thus not be determined with certainty. That its junction is posterior to the fronto-intertemporal joint is almost certain. There is no point at which this large canal could have united with the parafrontal canal (*a*) anterior to the fronto-intertemporal joint without its having been very much constricted. From what I have been able to determine, it appears that the junction occurs on the dorsal face of the alisphenoid (1') immediately posterior to that foramen for the canal, previously described, in the frontal (1).

The main infraorbital canal (*b*) runs almost vertically downwards through the postorbital (23), turning forwards into the suborbital (48) at the anastomosis of the hind end of the canal in the latter with the lower end of the canal in the former.

There are several main subsidiary branches of the canal in the postorbital: four on the anterior upper portion and three posterior, with numerous smaller channels which cannot be determined with accuracy. The infraorbital canal (*b*) now runs forward through the suborbital (48) to join the parafrontal canal (*a*) in rostro-nasal 18. In the suborbital are numerous branches of all sizes. Only those shown in the figure are fairly accurately determinable. The suborbital is porous and canalised, so that all parts of that region must receive some supply from the main canal. There appear to be 15 main sensory organs in the course of the infraorbital canal.

JUGAL CANAL (*d*) AND PREOPERCULAR CANAL (*g*).

(Text-figs. 5, 17, and 18.)

At the anastomosis of 23 and 48, the anterior limb of the squamosal (24) anastomoses also and carries posteriorly the main jugal canal. The posterior limb of the squamosal has large side apertures and many smaller openings, and there are two main inferior pores below the anterior limb. The canal runs through the squamosal and curves down to emerge on its lower edge directly into the canal in the upper anterior edge of the limb of the preopercular (25). In the preopercular the canal runs vertically downwards, to emerge near the hinder part of its lower edge. In the preopercular (25) are several determinable large branches and a number of finer channels and canals. From its emergence from the preopercular the canal is carried in a wide tube in the thick skin enfolding the lower jaw, and curves down and back over the lower outer face of the quadrate (34).

MANDIBULAR CANAL (*e*).

(Plate XXV; text-figs. 5 and 9.)

This originates in the upper hinder portion of the angular (29), where the dermal canal from the preopercular curves forwards abruptly, to run obliquely downwards towards the lower margin of the angular. The canal then continues forwards in the angular very close to the lower outer margin of that bone. From the main canal there are very many side convolutions into the angular-gular articulation groove which are not shown in text-fig. 5. That portion of the otherwise solid angular is much excavated into channels and grooves roofed externally by membrane (Plate XXV). There is a line of large pits in the bone just above, and communicating with, the canal.

The canal (*e*) passes from the angular into the splenial (30), in which it runs at first within the lower outer margin, but rises anteriorly to emerge higher in that bone, and thence to the symphysis. I cannot determine whether the two canals (*e*) meet across the symphysis.

From the main canal is a hinder branch which runs along the lower surface of the angular almost to the hind margin of the exposed portion. The canal comes to the surface at the hinder end, opening as a posteriorly diminishing excavation roofed by membrane (see text-fig. 5).

OLFACTORY ORGANS.

(Plates X, XI, XII, XIV, XV, XXI, XXII, XXV, and XXVII;
text-figs. 4, 6, 7, 11, and 15.)

In the ethmoidal region, just below the surface, lies a median cavity or sinus (R) whose apex is 24 mm. from the tip of the snout. This sinus is contained in the ethmoidal cartilage, and is roofed by a thin layer immediately below the gap between the fronto-rostrals. It is more or less depressed biconical in shape, 58 mm. in length, 19 mm. greatest depth on the mid-line, and about 35 mm. in width. The hinder part of the floor is a thin layer of cartilage which roofs the cranial cavity containing chiefly the optic lobes (L) of the fore-brain. The side of the hinder end of the sinus R is overlapped by frontal bone 2. Into it (R) lead six tubes from external openings. Anteriorly are two, one (A) from each side of the front of the rostrum. There are on each side two lateral apertures (B and C), placed much as the usual external nostrils of Teleosts, on the side of the snout before the eye, one above and behind the other. All six tubes are simple, and the openings are plain, without dermal fringes or cilia. The inner parts of the tubes and of the sinus appear to have had a membranous lining, with somewhat rugose or ridged surface. The most

careful examination of the walls of the central cavity has failed to reveal the faintest aperture or opening through the cartilage other than the three tubes on each side. The innervation of the membranous lining appears to be from the ophthalmic branch of the V nerve as described below.

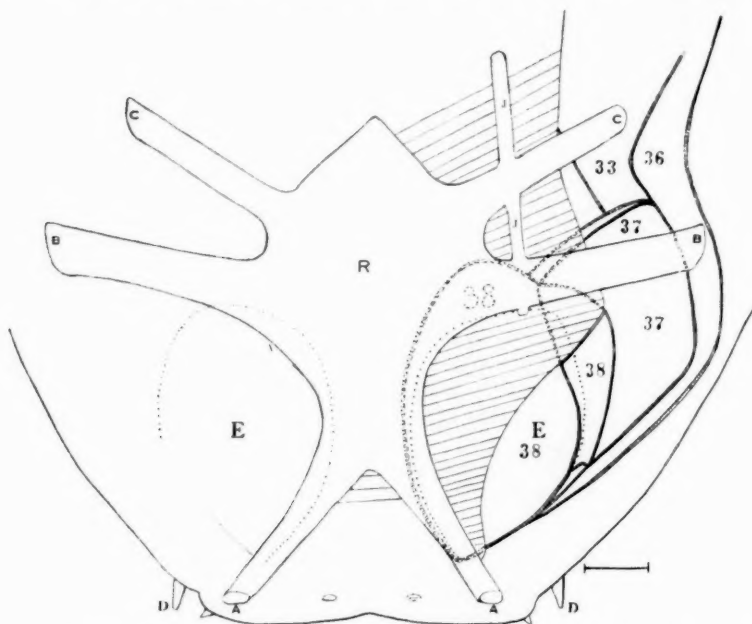
The rostral aperture (A) lies near the lateral edge and is 3 mm. in diameter. Inward from this aperture on each side of the front of the rostrum is a pit of slightly smaller diameter (see Plate XII) which marks a surface pore in the rostral commissural canal (*g*). The tube from each rostral opening curves upwards and inwards, running beneath the rostral commissural sensory canals (*g*, *h*, and *r*) and along the inner wall of the olfactory capsule (text-figs. 3 and 6), dilating posteriorly, the two openings being adjacent in the cavity R. The lower anterior lateral opening (B) is 8 mm. in diameter, slightly ovoid. It runs straight to the cavity slightly forwards, dilating inwardly. The first part of the tube is formed by an inner projection of the skin of the head merging into softer tissue within, which joins the margin of the ethmoidal cartilage, through the lateral flange of which the tube continues to the central cavity. The tube B runs below the lateral margin of the parafrontal-antorbital series of bones and above the head of the columnar lateral process of the ectethmoid (38). It had been suggested by Stensiö that in some forms the narial tubes may have passed through foramina in the antorbitals. His later withdrawal of that view is more in line with what I observe in *Latimeria*. The lower tube is about 35 mm. in length.

The upper tube (C) is about 25 mm. removed from the lower. The aperture and the tube are of slightly smaller diameter and shorter than B. The tube is of construction similar to the lower, but runs more obliquely forwards, through a tube in the ethmoidal flange as for B.

Running longitudinally along the flange of the anterior chondrocranium is a narrow tube (J) which I take to be the canal for the ophthalmic branch of the V and probably also the VII nerve. This canal opens into the upper narial tube (C) close to the median capsule (R), is continued between the tubes B and C, and appears finally to dip into the olfactory capsule. I am not certain of the latter as the cartilage in that region had been pulled about.

This system is difficult to interpret. Whether or not it has any affinity with the medio-dorsal olfactory system of Cyclostomes I am not prepared to say. That it now has no ventral connection, and shows no sign of ever having had any, with any part of the brain is certain. It is probably significant that the only part of the ethmo-rostral area not covered by bones is the roof of this ethmoidal cavity (R). There are no flaps to control or prevent the entry of water, and the membranous lining of the tubes does not appear to have been erectile or ciliate. Water would thus have free

entry through the tubes into the sinus R. When the fish moves forwards through the water, a current will pass through the rostral aperture (A), through the cavity, and out at the sides *via* tubes B and C. When the fish turns to one side, a contra-current will tend to flow through this



TEXT-FIG. 6.—*Latimeria chalumnae* Smith. Dorsal view of rostro-nasal area. The ethmoidal cartilage is cut away above the level of the narial openings. Cartilage shown by parallel line shading. Bones are outlined by cross-hatched double fine lines. The olfactory capsule is outlined by dots. The line represents 1 cm. For explanation see Folder-page I at end.

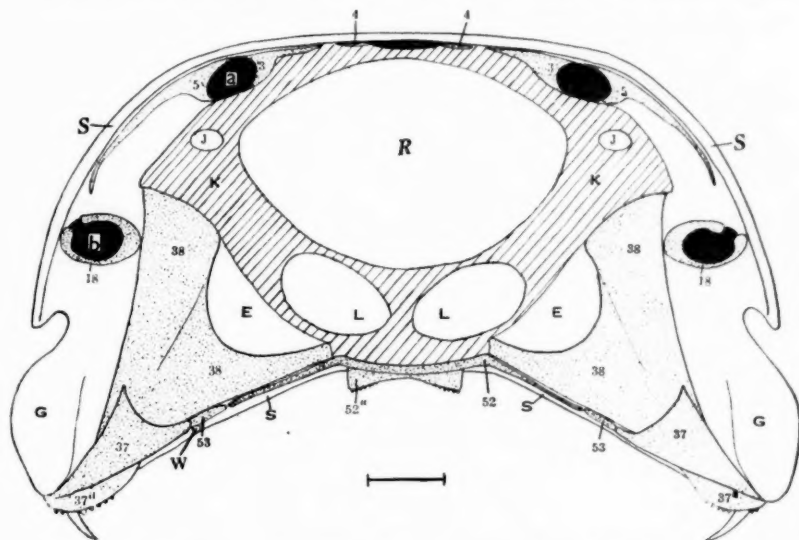
system. The whole may represent some form of sensory system, but exactly what may possibly not be decided until embryonic stadia become available for study.

The olfactory capsules (E) lie on each side of the snout, with anterior edge 10 mm. from the front margin of the rostrum. Each is a sac about 25–30 mm. longitudinal diameter, 25 mm. in width and about 25 mm. in height. Each is separated from its antimere by about 12 mm. across the upper surface of the parasphenoid (52).

The floor, the outer, and part of the hinder wall of each sac rests against the inner surface of the ectethmoid (38). The anterior face of the sac is

supported by the rostro-nasal (18), which rests against the anterior margin of the columnar process of 38. The inner hinder wall is in the rostral cartilage. There is a foramen above and behind communicating with the optic lobe of the brain (L) for entry of nerve I.

In so far as I can determine there is no external opening on any part of the head which communicates directly with these capsules. The lining membrane in the left capsule was in a bad state, being rather noisome and



TEXT-FIG. 7.—*Latimeria chalumnae* Smith. Transverse section of head 40 mm. from snout tip (see text-fig. 15). Cartilage shown by parallel line shading. Sensory canals black. Bone sections dotted. The line represents 1 cm. For explanation see Folder-page I at end.

partly glutinous and oily. It appeared in some degree to have been convoluted. Although the tissues had been rudely torn, I was able to trace a tubular structure of relatively fine tissue emerging from the capsule (E) through an aperture which exists above the lateral limb of the rostro-nasal (18), where it rests against the face of the outer column of the ectethmoid (38). This aperture is shown in text-fig. 11. The tubular structure runs outwards and laterally along the upper surface of the lateral limb of 18. What it is I could not with certainty determine. It may have been an anterior branch (optic-nasal) of the carotid artery.

ROSTRAL TENTACLE (CIRRUS) (D).

(Plates XI and XII; text-figs. 6 and 10.)

On each side of the rostrum is a flattened truncated conical cirrus or tentacle (D). Each is set in an oval base. The tentacle is 9 mm. in length and 4 mm. in width at the base. It is apparently imperforate. I can find no connection between this and any internal structure. It occupies much the position of the nasal cirrus found at the posterior margin of the oro-nasal groove in certain Selachians.

STRUCTURE OF THE MANDIBULARY RAMI.

(Plates IX, XI, XIV, XV, XXI, XXII, and XXV;
text-figs. 5, 8, 9, 11, and 13.)

The mandibulary rami are composite in structure, and have a lateral profile length of 250 mm. The quadrate articulation is anteriorly 190 mm. from the tip of the lower jaw in profile.

The outer surface of each ramus is formed chiefly by, posteriorly, an elongate angular (29) which covers the outer lower margin, and anteriorly by a similar but shorter splenial (30) which extends almost to the symphysis. Each of these structures is externally convex, fairly stout with an interior cartilaginous lining which, in the case of the angular, lines the adductor fossa (O).

Anteriorly, supero-internally, is the dentary (44) which appears to be, at least superficially, partly cartilaginous. Originating 50 mm. from the symphysis of the lower jaw is an elongate plate with anteriorly strongly convex edge, the articular-prearticular plate (43) which forms the inner, almost vertical surface of the lower jaw. The lateral face of the articular-prearticular plate (in the adductor fossa) is lined with cartilage.

On the inner hinder edge of the dentary (44) is the small precoronoid (40). Posteriorly is the elevated coronoid (41) whose inner surface dentition is extremely feeble. 25 mm. in profile behind the symphysis of the lower jaw there originates a stout external dermal labial fold (X) which extends, thickens, and broadens posteriorly, rising towards the coronoid (41), where a fossa on the outer side of its hinder margin receives the ligamental attachment from the inner face of the hind portion of the pseudo-maxillarial fold (G).

Chiefly between the angular and the prearticular plate (43) lies the extensive adductor fossa (O), which extends from in advance of the pre-coronoid (40) to almost beneath the quadrate articulation, having an approximate length of 140 mm. Its depth is approximately 18 mm. immediately in advance of the quadrate articulation, and it tapers to an

apex anteriorly. The fossa is roofed anteriorly by the inner fold of the labial cartilage.

Immediately anterior to the quadrate articulation the ramus of the lower jaw is 33 mm. in cross-section and 40 mm. in height. The lower surface of the lower jaws is covered almost entirely by the two very large and heavy gular plates (31), that on the left overlapping the right along the mid-line. These plates extend posteriorly to the level of the hind margin of the articular (32) and anteriorly to within 35 mm. of the symphysis, with a slight groove between the anterior limbs. For the greater part of the lower surface the gular plates overlap the lower margin of the angular (29). Anteriorly the gulars curve sharply inwards to their apices, so that between their anterior margins and the hinder margins of the splenials (30) is left a broad arrow-shaped area of thick folded skin which invests the anterior bevelling of the gulars. Just beneath the symphysis of the lower jaw originating 10 mm. from the apex is a fairly deep medio-longitudinal groove 6 mm. in length.

The articular (32) is comparatively short, at the maximum 60 mm. in length, and forms a bridge posteriorly between the angular and the articular plate. Time has not permitted me to ascertain the exact boundaries of the articular.

ANGULAR (29).

(Plates IX, XI, XIV, XV, XXI, and XXV; text-figs. 5, 8, 9, and 13.)

The externally convex angular (of the left side) is 170 mm. in length and 40 mm. greatest depth, which occurs midway along its length. It is a massive bone which forms the main foundation of the hinder part of the mandibular, and is 14 mm. in average thickness. The lower exposed margin of the bone is almost straight, and rises posteriorly and anteriorly to sharply rounded ends. The upper edge is undulate, rising from the anterior edge with gentle anterior concavity to a convex elevation midway where the bone is deepest. Thereafter the margin slopes downwards with gentle concavity, to meet the hinder end with a very slight, sharp convexity immediately below the outer ridge of the quadrate (34).

All the upper and most of the outer surface of the angular is smooth, with very fine radial striae and minute pits, but it bears no ornamentation in the form of tubercles, nor is there any indication that those were once present. There is little doubt that the whole upper length of the bone, with the exception of the posterior oblique entry tube of the mandibular canal (*e*), is solid. The lower margin of the angular bears the mandibular canal (*e*) (text-figs. 5 and 9), and above the line of the canal are several grooves and pits roofed by membrane. The lower margin of the bone is fairly elaborately sculptured. On the hinder lower surface the posterior

extension of the mandibular canal merges into a superficial groove, deep anteriorly, becoming shallower posteriorly, eventually rising to the surface of the bone. This groove is for its entire length roofed by strong membrane which merges into the skin behind.

The angular of the right side is 160 mm. in length and of maximum depth 38 mm. It is almost exactly similar to the left angular, except that there is medially a fairly large pit-groove structure which has a dorsal branch. The external surface of the angular appears to consist of ganoin. The centre of radiation appears to be exactly midway over the upper portion of the mandibular canal (*e*).

The upper portion of the angular is expanded across the mandible immediately in advance of the base of the quadrate (34), and forms the hinder face of the anterior margin of the quadrate articulation facet (text-fig. 13). Posterior to the quadrate the angular continues backward (text-fig. 13) for 46 mm., curving inwards beneath the skin, becoming apically fairly acute and progressively thinner. In this portion it forms the base upon which the relatively short articular (32) rests.

SPLENIAL (30).

(Plates IX, XI, XIV, XV, XXI, and XXV; text-fig. 5.)

The left splenial is 73 mm. in length and 19 mm. in greatest external width. It lies beneath the dentary (44), and is similar in structure to the angular (29) with smooth outer surface above, bearing fine radiating grooves and pits.

The mandibular canal (*e*) runs just below the mid-line of the splenial to near the anterior end. There it rises to emerge through the middle of the apex of the splenial, travelling thence to the symphysis. It appears to communicate across the symphysis, but time has not permitted the necessary dissection. The lower margin of the angular has, especially anteriorly, fairly numerous grooves roofed by membrane. There is a deep antero-exterior excavation with a membranous roof which is a dorsal expansion from the canal.

The centre of radiation appears to be located on the canal nearer the anterior than the posterior margin of the bone.

ARTICULAR (32).

(Text-figs. 8 and 13.)

Owing to the lack of time it has not been possible to make a complete dissection so as to expose the full extent of the articular. It is, however, a relatively small structure apparently confined to the post-quadrate portion of the mandible. The pre-quadrate rampart of the articulation

is almost certainly formed by the angular. The hind face and probably part of the floor of the articulation fossa for the quadrate are formed by the articular. The greatest length of the articular would appear to be 42 mm. and its greatest width about 21 mm. It is thickest anteriorly, its width and height tapering posteriorly to a blunted rounded hinder apex approximately 12 mm. in height, with inner face sloping inwards and downwards.

In the upper surface immediately in advance of the hinder apex is the cartilage-lined facet for articulation with the foot of the symplectic (39). This facet may clearly be seen in the inner portion of the articular of a specimen of *Diplocercides kayseri* (v. Koenen) figured by Stensiö ("Devonian Coelacanthids of Germany," Kungl. Sven. Vet. Hand., 1937, 3rd ser., vol. xvi, No. 4, text-fig. 18, pls. i and iii). It shows above the inner articular plate behind the quadrate articulation. Stensiö gives (*ibid.*, p. 15, text-fig. 7) a drawing presumably from the fossilised remains shown in pl. iii, but has apparently not regarded this facet as being of any significance, since he does not show it in the text-figure. It is likely that this facet will be found on the inner hinder face of the articular of all Coelacanthids.

GULAR (31).

(Plates IX, XI, XIII, XIV, XV, XXI, and XXV; text-figs. 5 and 9.)

The gulars are 225 mm. in total length and 70 mm. maximum width, which occurs about the middle of their length. The outer surface of each gular is ventrally convex, the transverse convexity having a faint broad anterior ridge, the longitudinal convexity being comparatively slight.

The plates are not more than 4 mm. in thickness and lie immediately beneath the skin of the floor of the mouth. In general shape each gular is more or less fusiform but with each apex pushed over towards the inside, anteriorly more than posteriorly. The inner margin runs almost straight from the apex posteriorly, then curves out a distance of 15 mm. to the posterior apex. From the posterior apex the outer margin is broadly convex, and runs in a gentle curve to the widest part of the bone. Thereafter the gular narrows anteriorly to about 35 mm. behind the apex, when the margin curves inward to the apex forming an anterior concavity.

The left gular overlaps the right for about 4 or 5 mm. for three-quarters of the length along the middle portion. Anteriorly the inner margins are separated 2 mm. apart for 22 mm. of their length. The outer surface of each gular is hard and fairly smooth, consisting apparently of ganoin. The surface bears very fine reticulate grooves and a dense system of minute pits. The grooves lie chiefly anteriorly along the outer margin and posteropically. The tiny pits cover most of the central (inner) portion of the bone.

The left gular shows no trace of tubercle ornamentation. There are in its surface several large deep excavations on the anterior third and towards the centre, all roofed by membrane. These are not definite "pit-lines," but communicate with deep and extensive sensory cavities within the bone. I cannot trace any other sensory organs in either gular.

The right gular differs from the left solely in possessing two isolated pairs of small tubercles on the lower surface, and in having the roofed pits slightly nearer the outer margin than those on the left. The outer margins of the gulars are trenchant. They appear to be much thicker anteriorly.

CORONOID.

(Plate XXI; text-figs. 8, 9, 11, and 13.)

The coronoid is situated with the anterior margin 100 mm. from the tip of the lower jaw. It is somewhat trapeziform, roughly in the form of a truncated triangle with undulate base and sides. The structure is 40 mm. in height, 65 mm. in length, and but 2-3 mm. thick at the thickest point, which occurs at the lowest anterior portion (left coronoid).

On the anterior lower part of the face is a granulate plate, more or less hastate in outline, with apex posterior, 37 mm. in length and 14 mm. in height. Above this plate the inner face of the coronoid bears small blunt tubercles, slightly larger posteriorly. The main structure is hard, apparently well ossified, and may even bear ganoin on its inner face.

In transverse section the coronoid slopes inwards and downwards, the interior face being concave above and convex below (text-fig. 9). The basal margin of the coronoid articulates with the upper edge of the articular-prearticular plate (43). The upper edge of the structure is gently convex and firmly attached to stout connective tissue. The pseudo-maxillarial fold (G) is joined into a posterior fossa in the hind margin of the elevated expanded hind portion of the lateral labial fold, which ends beneath the anterior corner of the upper portion of the coronoid.

The coronoids probably add very considerably to the strength of the jaws. They would effectively prevent any lateral play between the upper and lower jaw when the mouth is closed or almost closed. The typical raptorial nature of the dentition, and the obvious provision for very large jaw muscles, would indicate that prey once seized could never escape.

MOUTH.

(Plates I, X, XI, XII, XIV, XV, XXI, XXII, and XXV;
text-figs. 5, 7, 8, 9, 10, 11, 12, 13, 15, 16, and 17.)

The mouth is large, terminal, horizontal, with lower jaw projecting slightly. The gape extends to below the hind margin of the eye, 160 mm.

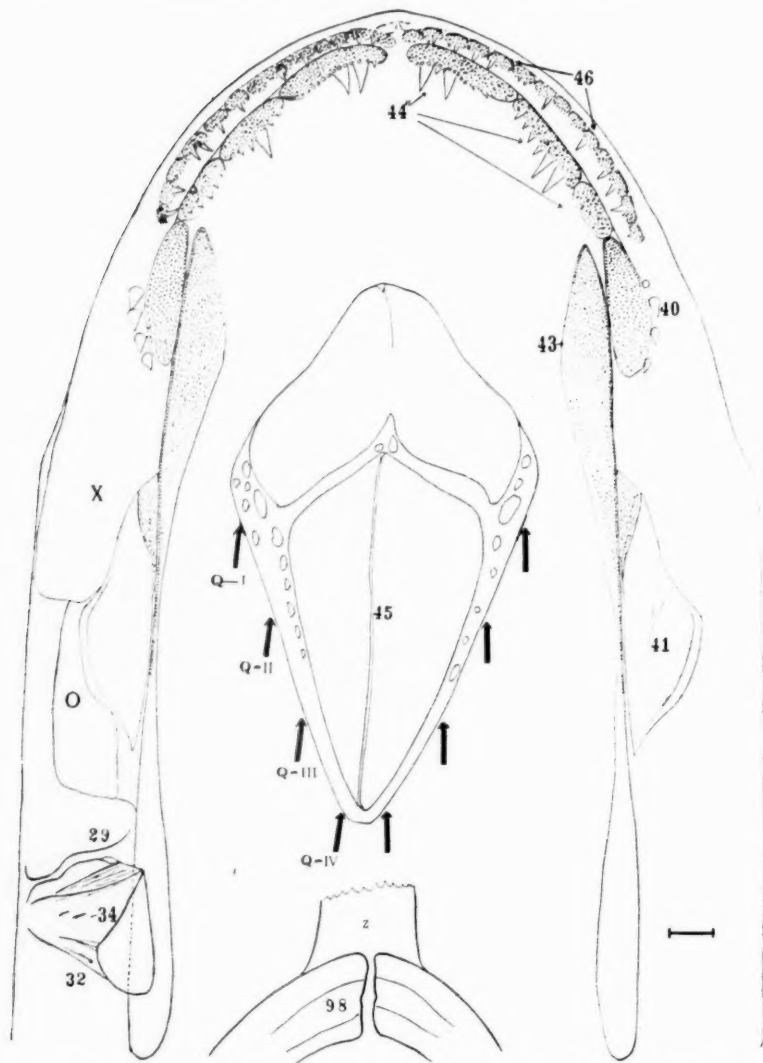
from the snout tip measured obliquely. Width at hind angle 160 mm. The dentition is raptorial and fairly powerful. The most powerful dentigerous structures are the plates held by or upon the prevomers (53"), the palatines (37"), the ectopterygoids (36), the dentaries (44"), and the precoronoids (40). The teeth are all conical, ranging from small, blunted basal granules to large prominent tusks. Mostly each dental plate is composed of the coalesced bases of small or moderate teeth, which increase in size towards the mid-portion of the inner margin of the plate, where usually two large sharp tusks form the chief dentition. Only in the case of the hinder part of the ectopterygoid do the teeth appear to be implanted directly in that bone. The dental plates are in some cases superficial only, being held by the thick skin of the mouth (90, 91, 46).

There is evidence that replacement of teeth is successional, since in several of the dental plates where a large tusk has obviously recently been lost, a similar but smaller retrorsely depressible tooth appears to be moving upwards in replacement.

LOWER JAW.

(Plates IX, X, XI, XII, XIII, XIV, XV, XXI, XXII, and XXV;
text-figs. 5, 8, 9, and 11.)

The lower jaw has massive rami, the gular plates (31) providing additional strength. On the upper external surface of the dentaries is set in the skin a series of twenty-seven small dental plates (46), which represent the anterior portion of the labial fold. On the left dentary are thirteen plates, on the right fourteen. The bases of the plates are contiguous, with a break at the symphysis. The plates are oval, 5-6 mm. in width and about 3-4 mm. in average depth, and are very firmly fixed in the extremely tough skin of the "lips." Each plate is composed of close-set, basally coalesced small conical teeth 1-3 mm. in length. Of the plates on the left dentary, nine bear in addition posteriorly a larger curved caniniform tooth about 4 mm. in length, one bears two such teeth, the remaining two having only small teeth. On the right dentary eight plates bear each a single larger tooth, while four bear pairs of larger teeth, the remaining two having only small teeth (text-fig. 8). Immediately internal to these "labial" teeth, and running behind them, is on each side a system of three exactly similar, but much enlarged, plates (44"). On each side of the symphysis is the anterior plate of the dentary. The length is 24 mm. and transverse width about 6 mm., with outer margin convex. The basal teeth are externally fine, somewhat blunted. They increase in size inwards, finally forming a posterior medial ring, the apex of which stands about 6 mm. above the lower margin of the external edge of the base. Behind



TEXT-FIG. 8.—*Latimeria chalumnae* Smith. Dorsal view of lower jaw showing quadrate articulation. Small teeth shown by dots which are not accurate as to number. The position of the tuberculate copula is approximate only. The large arrows behind the copula show points of attachment of the branchial arches. The line represents 1 cm. For explanation see Folder-page I at end.

this rampart, slightly to the inner side, are inserted two large tusks, each about 9 mm. in free length, which are directed obliquely upwards and inwards. The second pair of plates, the medial supradentaries, originate 33 mm. radially on each side from the symphysis. The left plate is 20 mm. in length and 5-6 mm. in transverse width. Behind the central rampart are inserted five larger teeth, the central being much the largest, the outer two pairs being graduated smaller. The right plate is 23 mm. in length and 5-6 mm. in width. There are six enlarged teeth along the hinder margin. The posterior two are large tusks, directed inwards and upwards, while the remaining four are graduated smaller anteriorly. The outer posterior pair of supradentaries is the smallest. Each originates 53 mm. radially from symphysis, is about 16 mm. in length and about 6 mm. in width. The right plate has only small teeth. That on the left has an inner series of five moderate, stout, conical teeth, the centre one being the largest, the outer graduated shorter, all directed inwards and upwards.

The marginal dentition is completed by that on the precoronoids (40), which originate radially about 70 mm. from the symphysis, where the transverse width of the lower jaw is about 120 mm. On the inner face of each precoronoid is an oval basal plate, 30 mm. in length and 14 mm. maximum height, which bears close-set small denticles. Above and external to the hinder upper edge of the denticulate plate are large conical teeth in a single series. On the left side there are four large tusks, the anterior the largest, directed obliquely backwards, the hinder teeth graduated rather smaller and increasingly more retrorse. On the right precoronoid are also four somewhat smaller teeth, the anterior almost vertical, the posterior three directed backwards, the hindmost almost prone.

Still further posteriorly lie the large more or less trapeziform coronoids (41), which have been described elsewhere.

The inner surface of the lower jaw is formed by an elongate denticulate plate with subvertical surface, the articular-prearticular plate (43). The anterior end is rounded and originates below the hind end of the posterior supradentary. The plate is 180 mm. in length and 40 mm. average depth, with a convexity below the basal denticulate plate of the coronoid. The plate extends backwards beyond the quadrate articulation, to the anterior margin of the articulation facet for the symplectic (39). The anterior part of the face of the plate (43) is dentate, the denticles along the anterior and upper margins being the greatest. Posteriorly and inferiorly the denticles become smaller, until finally, 90-100 mm. from the anterior end, they merge into fine striations which become obsolete posteriorly. The posterior part of the face of the plate is almost quite smooth.

On the floor of the mouth only part of the original skin has been left.

Anteriorly are a few small dermal plates bearing denticles resembling those on the copula (45). On the floor of the mouth is the tuberculate copula. This structure had been removed before I saw the specimen, and the severed skin on the floor of the mouth does not assist very much in orientating the copula. I can only suppose the tubercles on the copula to have opposed the parasphenoid plate (52"), since it fits fairly well against that. The copula is shown in text-fig. 8, but its position there is only an approximation.

COPULA (45).

(Plates XXIII and XXIV; text-figs. 8 and 9.)

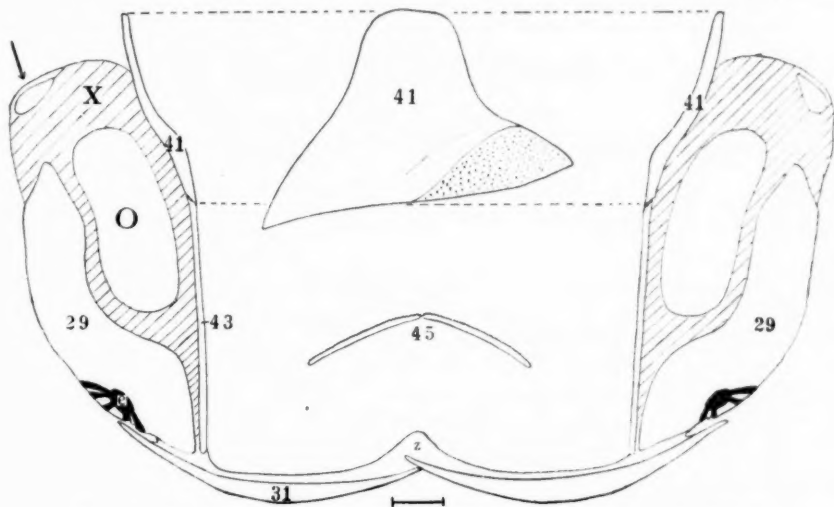
The copula is a composite ossification, consisting chiefly of a laminate superiorly convex tuberculate roof of four fused plates. It was stated to have had the appearance of a free "tongue" in the floor of the mouth. The total length of the structure is 118 mm. and its maximum breadth is 58 mm.

The upper surface is formed by the fusion of two pairs of plates. The anterior pair form a blunt arrow-head with median suture of about 30 mm. in longitudinal length. The hinder pair with median suture form a hastate hind limb whose apex fits into the recess in the "arrow-head." The hind plates are each about 80 mm. in length and 28 mm. in width at the widest part, which occurs anteriorly. The whole surface is hastate, with apex posterior. The four plates are densely covered with somewhat elongated tubercles in more or less regular radiating rows. Those on the anterior pair radiate out in regular rows from the apex, while on the posterior plates the tubercles radiate out in all directions from an area midway along the inner margin of each plate. Posteriorly on the structure the tubercles become so close-set as to resemble longitudinal striae. The four plates appear to have originated from scale-like entities. The margins of the plates are bound to thick skin such as remains marginally on the floor of the mouth. On this skin, marginal from the anterior edge of the hinder plates, are small dentate or granulate plates of irregular size and shape, which are similar to those on the floor of the mouth. They are patently but modified scales.

Transversely the copula is arched, the sides sloping at about 15° downwards from the horizontal (text-fig. 9). In longitudinal section the copula is almost straight.

As mentioned previously, the copula had been removed from the buccal cavity during mounting, and the taxidermist cannot give much information about it, except that it was visible from the front of the mouth, that it was part of the gills, and that the gill-arches were attached to its lower surface. I judge that the structure was set up in the mouth sloping upwards and

backwards at an angle of about 30° to the horizontal, so as to present a surface to articulate with the parasphenoid plate (52°). Below the angular suture between the posterior and anterior plates is a light, ossified, more or less pyramidal box-like structure, either hollow or very poro-cancellate within. It probably represents a basi-hyal or glosso-hyal. The hollow ossification has been enveloped in cartilage. It is 48 mm. in length, 44 mm. in width, and 22 mm. in height. It bears a circular depression, 21 mm. in diameter and about 8 mm. in depth, on its hinder face. I take this to



TEXT-FIG. 9.—*Latimeria chalumnae* Smith. Transverse section of lower jaw 130 mm. from symphysis. Cartilage shown by oblique line shading. Dentate area dotted. Central (above) is view of coronoid from within the jaw. The arrow shows the fossa for attachment of pseudo-maxillarial fold (G). The position of the copula is approximate only. The line represents 1 cm. For explanation see Folder-page I at end.

be a facet for articulation of possibly a hypobasibranchial. Below this depression is a transverse rectangular facet, 28 mm. in width and 4-5 mm. in height, which is probably the articulation facet for the head of the uro-hyal. On the anterior face of the hollow ossification is a median cartilaginous ridge which bifurcates anteriorly, i.e. just below the roof of the copula, into two dilated rounded branches. On each side is thus formed a moderate fossa against the median ridge, which may be the points of articulation of the anterior inner faces of the cerato-hyals. Very similar, in fact almost identical, is the structure shown by Nielsen (Prelim. Rem. Trias. Fishes, East Greenland, Medd. Grøn., 1936, Bd. 112, Nr. 3, pp. 33-34, fig. 16) in a large unidentified Coelacanthid from East Greenland.

I cannot find any signs of the wide longitudinal canal stated by Nielsen to be present in his material.

Along the margins of the lower cartilaginous backing of the hinder plates of the copula are clearly to be seen the points to which on each side four cartilaginous structures, presumably gill-arches, were attached. The number is certainly four and not five. I should judge that they were superiorly attached to the copula, and probably bound more closely together by attachment to a rod-like, possibly entirely cartilaginous, basibranchial, whose head would articulate in the circular fossa in the hind face of the basi-hyal.

No traces of a cerato-hyal remain in the fish.

UPPER JAW.

(Plates XI, XII, XIV, XV, XXI, XXII, XXV, and XXVII;
text-figs. 5, 7, 10, 11, 12, 15, 16, and 17.)

The most striking feature of the upper jaw is the absence of maxillae and of premaxillae. The external appearance of the upper jaw suggests that maxillaries are present. This is due to the presence of a thickened fold of skin here termed pseudo-maxillarial labial fold (G), which originates on the outer face of the base of the ectethmoid (38), and extends along beneath the lower edge of the suborbital (48). The hind end of the structure, from within its rounded apex, is connected within a fossa in the hinder upper portion of the cartilaginous lower labial fold (X) (see arrow, text-fig. 9). Externally this structure resembles a conventional maxilla very closely. Its presence suggests that there has never been a "loss" of a maxilla in any ancestral form, but rather that in that ancestral form the structure of maxillarial homology failed to develop by ossification. In its hinder third this fold is 24 mm. in depth and 8 mm. in average thickness. It is extremely tough, being enclosed outside, below, and within by extremely hard skin, though it shows no sign of ossification. The central portion in a section has a structure similar to that shown for the skin of the cheek in Plate XLIV.

Most of the teeth in the upper jaw are borne by dermal plates. In some cases these are set in the skin, in others they appear to be fused to the lower surface of the palatal bones. Only in the hinder part of the ectopterygoid are there any teeth set directly in a palatal ossification.

The comparatively slight vertical bones in the rostrum (20, 21, and 22) do not resemble either a developing or an obsolescent premaxillary. The rostral dental plates (90) are purely superficial structures without definite relationship to the rostrals (20-22), except that they lie about 4-5 mm. beneath them in the skin. The total width of the rostral projec-

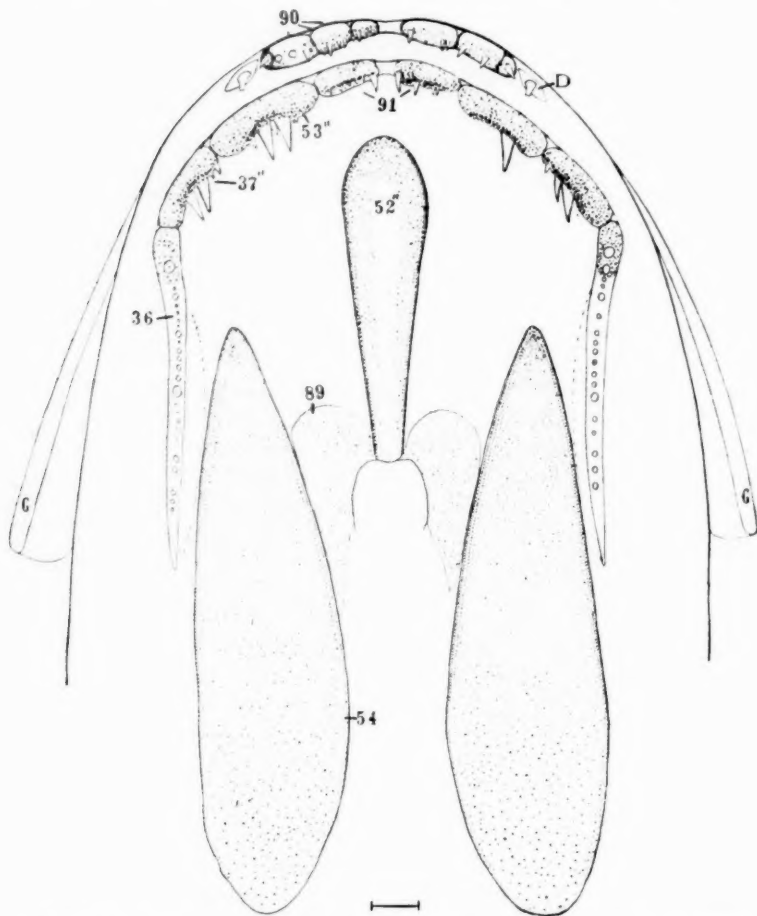
tion is 55 mm. The lower surface is divided into two lateral segments by a moderate groove 5 mm. in width. On the left section are four dental plates. Externally is a small stud-like plate with a moderate conical tooth centrally and a smaller one anteriorly. The next plate is largest, 10 mm. in length, and bears three conical teeth which are directed downwards, radiating slightly. The second lateral tooth is the largest, 4.5 mm. in length. The plate is smooth anteriorly with a few basal denticles. The middle plate is 8 mm. in length and bears four teeth smaller than those on the outer plate, but is otherwise of similar structure. The inmost plate is only 6 mm. in length and bears three small conical teeth directed obliquely backwards. On the right section of the rostrum also are three plates. The outer is but 4 mm. in diameter and bears one conical tooth, 5 mm. in length, directed outwards and backwards. The right median plate is 9 mm. in length and bears two conical teeth directed almost horizontally inwards. The inner plate is 13 mm. in length and has two moderate conical teeth on its lateral portion, a larger tooth on the opposite side and a smaller tooth midway between, all directed obliquely inwards. All plates are smooth anteriorly, with blunted denticles at the bases of the larger teeth. Many of the exterior denticles are merely tubercles exactly similar to those on the scales.

5-6 mm. behind the rostrals is the anterior part of the marginal dentition of the upper jaw. At the apex are two dental plates, 4 mm. apart across the mid-line, which are termed "post-rostrals" (91). These plates bear no relation to any palatal ossification. They are set in the skin of the mouth inward from, and slightly anterior to, the prevomers. Each is 14 mm. in length and about 5 mm. average breadth. On the right post-rostral are four fairly large, slender conical teeth directed almost horizontally backwards. The inner (4 mm.) is largest, the outer graduated smaller. The left postrostral bears one inner similar tooth (4 mm.), and more laterally are five smaller teeth, all directed inwards.

The dermal plates of the prevomers (53") are the largest in the upper jaw. They lie immediately outside the postrostrals. The right plate is 24 mm. in length and 6 mm. in width; the left 27 mm. in length and 7 mm. in width. On the right plate is one stout tusk, 12 mm. in length, inserted behind a rampart of stout low conical teeth. There had evidently been two such teeth, since the socket of another is visible, in which anteriorly a retrorse smaller tooth is clearly in process of upward succession. The left plate of the prevomer bears two large tusks (11 mm.) directed obliquely inwards. Between them and outside them are somewhat smaller similar teeth, all inserted behind a stout rampart of low conical teeth.

The palatine plates (37") lie postero-externally to the prevomers. The right plate is 21 mm. in length, the left 20 mm. Each bears two large

tusks (9 mm.) directed backwards and inwards, inserted behind a rampart of stout low conical teeth, one or two of which anteriorly are enlarged.



TEXT-FIG. 10.—*Latimeria chalumnae* Smith. Mirror image diagram of palate. Dentate areas dotted. Accurate to scale except for number and disposition of small teeth shown by dots. The line represents 1 cm. For explanation see Folder-page I at end.

The marginal dentition is completed by the ectopterygoids (36), which curve inwards from their origin behind the palatine plates and thereafter run straight along the lateral face of the pterygoids. Anteriorly each

bears a dermal plate. The right dermal plate bears two large fang-like conical teeth, the anterior the larger, both directed somewhat backwards, while the left bears a single large tusk (10 mm.) directed inwards. Behind the plate in each ectopterygoid is a single series of conical fang-like teeth of various sizes, apparently implanted directly in sockets in the bone itself. In the right ectopterygoid, behind the dermal plate, are anteriorly two small teeth, then one somewhat larger. There follow in succession six smaller teeth, a large tusk, two small teeth, and finally three moderate fangs. The left ectopterygoid has in its succession of teeth anteriorly a small canine, then a moderate fang-like tooth, four rather small teeth, another like the second, followed by a mere point, then four small fangs with two heavy tusks (8 and 7 mm. in length) behind. These are followed by three small teeth, then two somewhat larger, and finally by a posterior group of three smaller teeth. Each ectopterygoid is approximately 70 mm. in length within the jaw.

The parasphenoid dermal plate (52") originates 25 mm. behind the apex of the rostrum, and is about 70 mm. in length. It is more or less spatulate, anteriorly dilated, the maximum width 19 mm., occurring in the anterior third of its length. Posteriorly it is 6-7 mm. in width. The plate is concave beneath, along the median line. Its cross-section at various points may be seen in text-fig. 12. The plate is densely covered with granulo-conical teeth which diminish inwardly and posteriorly. Those round the anterior margin are enlarged, and robustly conical and sharp, forming a raised edge. The hinder granules are feeble.

The entopterygoid plates (54) are large. They are fairly thin and approximately triangular in shape, being set on the inner face of chiefly the anterior lobe of the pterygoid (33), thus facing inwards and downwards. (Text-fig. 10 shows their vertical projection.) They are about 130 mm. in length and about 45 mm. in oblique height at the maximum. The hind margin of the plate extends about 200 mm. behind the apex of the rostrum, to above about the middle of the quadrate (34). The whole outer surface is firmly adnate to the pterygoids. The dentition is feeble. Anteriorly along the margins are small blunted conical teeth in one or two series. Inwards from these are bluntly rounded denticles, anteriorly fairly close-set, diminishing in size and density of setting posteriorly. The posterior lobe of the plate is almost smooth.

Between the entopterygoids and the parasphenoidal plate is a dentate area of the skin, pointed posteriorly, with rounded anterior margin, about 40 mm. in length and 15 mm. maximum width, with margins abutting against the entopterygoid and the parasphenoidal plate. These areas are but feebly ossified if at all, the rather granular close-set teeth being apparently merely dermal denticles in the rather stout skin connecting

the pterygoid with the parasphenoid ventral face. I name these for convenience suprapterygoid (89) areas.

Between the dentigerous structures the roof of the mouth consists of extremely tough leathery skin, about 1.5 mm. in thickness, of very smooth surface. There is no sign of any internal narial opening. Between the pterygoids, behind the parasphenoidal plate, the hind margin of the parasphenoid and all of the ventral (mouth-roof) structures had been removed when the fish was mounted.

STRUCTURE OF THE DENTAL PLATES AND OF TEETH.

(Plate XXXII.)

This has been investigated by taking sections of the second (from without) rostral dental plate and of one of the teeth it holds.

The plate is rounded anteriorly, the front surface being almost edentate and fairly smooth. The hinder portion of the plate embedded in skin and cartilage is produced into a sharp ridge. The body of the plate is densely ossified, and marginally very solid. The teeth are implanted in fairly deep sockets, with rounded bottoms. Chiefly above each tooth, but all along the central core of the plate, are irregular sinuses, apparently interconnected, containing pulp or vascular tissue. The lowest of these communicates directly with the pulp-cavity in the tooth, while the most dorsal is right in the upper surface of the plate. This excavated portion is not of a spongy nature, the bony walls between the sinuses being quite solid. The whole suggests origin from the cosmoid type of scale.

The teeth are almost certainly derived from tubercles such as are present upon the body scales. On the front margin of the rostral plates are present all stadia transitional between low rounded tubercle and elongate conical tooth. In Plate XXXII a small tubercle may be seen in section on the front margin of the plate anterior to the main tooth.

The teeth themselves are hollow almost to the apex, and the pulp-cavity is rather large. The tooth is actually a hollow cone with a more or less hemispherical base deeply embedded in the body of the dental plate. The base beds on to and opens into the lowest irregular sinus of the body of the plate.

A transverse section of the tooth is a hollow cone. In fine section the body of the tooth has a radial structure, but no tubuli can with certainty be distinguished. The outer layer of enamel, except at the apex of the tooth, is rather thin. Under the polarising microscope the dentine shows slight birefringence with somewhat undulose extinction, suggestive of strain rather than of crystalline structure.

The elongate spines on the dermal plates of the inner surface of the

hyo-mandibular capsule (Plate XXX) are of structure similar to that of the teeth. They are rather more slender than the teeth, and the pulp-cavity is of relatively smaller diameter. The rostral (and jaw) teeth appear to have developed by extension of the upper portion of the tubercle, the buccal denticles by prolongation of the ends of the tubercles.

PALATO-PTERYGO-QUADRATE SYSTEM.

(Plates XXI, XXII, XXV, XXVII, and XXVIII;
text-figs. 6, 7, 8, 11, 13, 16, 17, and 18.)

This complex is massive, well ossified, and forms the principal foundation of the skull.

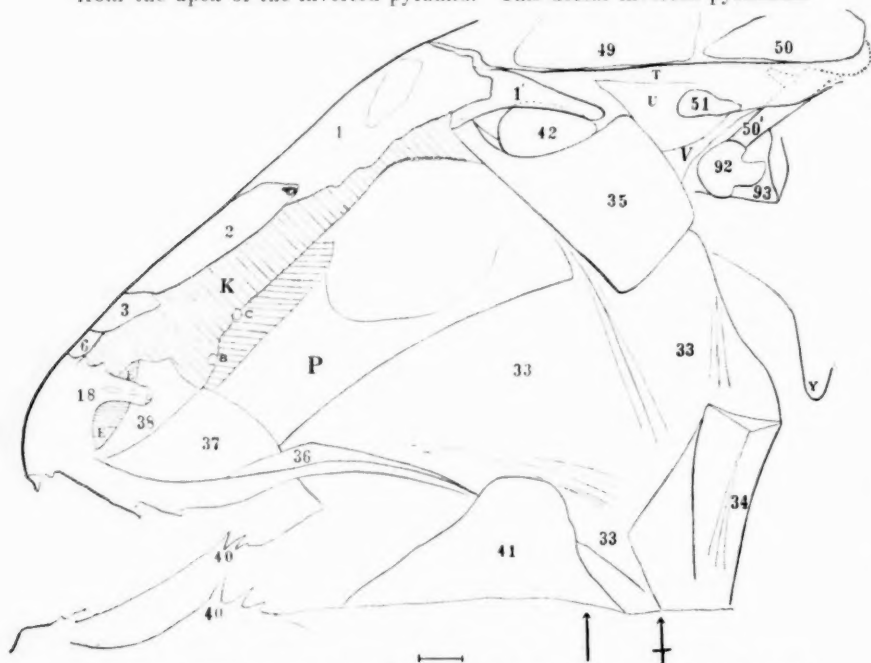
QUADRATE (34).

(Plates XXI, XXV, and XXVIII; text-figs. 8, 11, 13, and 18.)

The quadrate articulation occurs 185 mm. behind the tip of the lower jaw. The lower portion of the quadrate is typically expanded, and the condylous extremity is externally cartilaginous. The main limb of the quadrate is an inverted triangular pyramid of rather small base. The greatest height of the quadrate is 76 mm. The triangular upper surface is 26 mm. in length and 11 mm. in width (transverse). The hinder surface of the column slopes slightly backwards as a slight concavity. The anterior ridge of the triangular column is expanded into a ventrally wider laminate limb. The total width of the quadrate half-way up its length is 34 mm., the laminate expansion being 20 mm. wide at that point. On the outer upper face of the quadrate is a fairly sharp dorso-ventral ridge for half the columnar length, corresponding with one angle of the sectional triangle. The inner face of the quadrate appears to be gently rounded and lies mostly just external to the plane of the prearticular (43). The triangular dorsal face of the quadrate column is soft and porous and had obviously been connected by cartilage with the hindmost outer surface of the pterygoid (33). The inner face of the quadrate fits exactly on, and is marginally at least closely adhesive to, the exactly similar conformation of that portion of the outer face of the pterygoid, *i.e.* the lower hinder portion of the pterygoid (33). The quadrate and that portion of the pterygoid are very firmly bound indeed, so that it would almost appear as if the bones had fused within at least part of the contiguous surfaces. It appears that the cartilaginous attachment between the quadrate and the pterygoid may have a dorsal extension attached to the hinder lower corner of the metapterygoid (35), but since the cartilage (if there) has been removed this cannot be stated as fact.

There are indications that the quadrate ossification is in two separate

sections, the lower centre radiating out upwards through the anterior lamina, and also posteriorly along the outer hinder face of the triangular columnar process. An inverted pyramidal portion of the latter column appears to be a secondary or separate ossification with centre of radiation from the apex of the inverted pyramid. This dorsal inverted pyramidal



TEXT-FIG. 11.—*Latimeria chalumnae* Smith. Left side of head with lateral dermal and parafrontal structures removed. Cartilage shown by parallel line shading (see Plate XXI). The plain arrow marks position and angle of cross-section shown in text-fig. 17, the crossed arrow that shown in text-fig. 18. The line represents 1 cm. For explanation see Folder-page I at end.

process is cancellate within, and of lighter structure than the basal portion of the bone. There is an appearance of a suture along the anterior margin of this latter process.

METAPTERYGOID (35). (EPIPTERYGOID?.)

(Plates XXI, XXV, and XXVIII; text-figs. 11, 13, 17, and 18.)

The metapterygoid lies against the surface of the upper limb of the pterygoid; its lowest point is 47 mm. below the apex of the pterygoid. In shape the metapterygoid resembles a short-handled, broad-bladed

cleaver. The outer face of the bone is slightly concave, both longitudinally and transversely, the latter curvature having slightly the smaller radius. The anterior margin of the metapterygoid lies against the median columnar superior process of the pterygoid face. The lower portion of the bone fits closely against the outer surface of the hind limb of the pterygoid (33), and is so firmly fixed as to suggest inter-calcification or even partial fusion. This hinder limb of the pterygoid is so firmly fixed to both the quadrate and the metapterygoid as to constitute almost a single element.

The greatest length of the metapterygoid is 61 mm. and the greatest depth 41 mm. The ascending process (anterior) is directed forwards and upwards, viewed laterally, at an angle of about 30° from the horizontal. The apex almost articulates with the lower surface of the frontal (alisphenoid) (1') immediately beneath the anterior margin of the intertemporal (49). The upper surface of the metapterygoid is fairly thick, at the lowest point of the concavity it is 10 mm. in thickness. On this concavity, and connected thereto by strong tissue, lies the end of the antotic process of the basisphenoid (42), the rounded outer surface of which lies very slightly external to the plane of the outer face of the metapterygoid. To the apex of the anterior limb (*processus ascendens*) of the metapterygoid is joined the hinder upper corner of the frontoethmoidal cartilage, and immediately above this commissure originates the endochondral portion of the lateral canal (J) for the ophthalmic branches of the nerves V and VII.

The upper surface of the metapterygoid extends approximately 20 mm. above the margin of the hinder limb of the pterygoid. The hind margin of the metapterygoid is sharply convex and very porous except for the outer surface. Cartilage has obviously been attached along the greater portion of this edge, part of which may have been joined also to the quadrate. At the lower corner the metapterygoid is no thicker than 2 mm., but it thickens dorsally, chiefly antero-dorsally. The hinder edge is 4 mm. in thickness. The blunted apex of the anterior process is uniformly 9-10 mm. in thickness.

The front surface of the metapterygoid is inclined at an angle of about 30° from the vertical sagittal plane, and about 25° from the vertical transverse plane. The inner margin of the anterior apex is separated from its antimeric by 16 mm. The inner margin of the inner lowest point of the surface of the metapterygoid, upon which the antotic process (42) rests, is separated from its antimeric by 35 mm. The centre of radiation of the metapterygoid is not very obvious, but appears to lie near the base of the anterior ascending process.

The prootic (93) lies behind the middle of the metapterygoid, the hinder end projecting beyond the hind margin of that bone.

PTERYGOID (35).

(Plates XXI, XXII, XXV, XXVII, and XXVIII;
text-figs. 6, 11, 13, 16, 17, and 18.)

The pterygoid is by far the largest ossification in the head, and is broadly trilobate, the anterior lobe being the greatest, the hinder, lowest behind the quadrate the least. The greatest longitudinal length of the pterygoid is 156 mm. and its greatest height is approximately 112 mm. The radial centre of the structure lies immediately anterior to, and slightly below, the apex of the quadrate (34). The main foundations of the pterygoid are three stout columnar processes. The lower, about 125 mm. in length, runs almost horizontally towards the anterior apex of the structure, which articulates beneath the hinder lower surface of the autopalatine (37). The median process is about 90 mm. in length and runs at an angle of approximately 45° from the horizontal, upwards and inwards, to end beneath the upper portion of the metapterygoid (35). The hinder upper margin of this middle ridge is trenchant, and almost overlaps the anterior outer face of the metapterygoid. The posterior and stoutest process of the pterygoid rises posteriorly from the radial centre at only a slight angle from the vertical in all directions, and extends upwards curving behind the metapterygoid to meet the posterior flange from the median process of the pterygoid in a broad curve. The upper and hinder face of this hinder pterygoidal process is broadly bevelled posteriorly, the bevelling on the level of the marginal articulation of the metapterygoid being about 15 mm. in width downwards and backwards. The bone connecting the median and hinder columnar processes has a deeply concave surface, to the upper portion of which the lower limb of the metapterygoid is ankylosed. The laminate structure between the median and the anterior pterygoidal processes is triangular, with an obtuse angle against the median columnar pterygoidal process. The apical angle is approximately 100° , the base of the triangle is approximately 110 mm. and the height about 58 mm. The upper anterior margin of this lamina is very gently convex, viewed laterally is almost straight, with no notch or emargination. This triangular lamina is fairly deeply concave, the lowest point of the surface near the upper margin being 19 mm. below the plane joining the upper edges of the median and the anterior pterygoidal columnar processes. The radial curvature is comparatively slight.

Along the middle of the upper surface of the laminate process of the pterygoid the antimere lies 25 mm. away. The lower hinder lobe of the pterygoid lies exterior to the upper anterior area enclosed by the marginal columnar processes.

Below the anterior limb there is an inferior triangular portion of the pterygoid approximately 24 mm. in height and 55 mm. in longitudinal length to the anterior margin of the quadrate. The pterygoid at this point passes behind the quadrate, 15 mm. above the quadrate articulation of the lower jaw, and curves upwards and backwards to meet the outer flange from the hinder pterygoid process which runs downwards, its hinder extremity being coincident with the upper hinder edge of the columnar process of the quadrate.

AUTOPALATINE (37).

(Plates XXI, XXII, XXV, and XXVII; text-figs. 6, 7, and 11.)

The autopalatine is a prominent structure in the anterior portion of the upper part of the palate. In lateral view it is an almost equilateral triangle, with side 38 mm. in length and base 41 mm. Externally the hinder portion is overlapped by the ectopterygoid (36), while internally the autopalatine overlaps 14 mm. of the apex of the anterior limb of the pterygoid (33). The outer face of the autopalatine is longitudinally almost plane, but the profile transversely is deeply concave. There is a lateral inferior limb of convex margin which forms part of the border of the upper jaw, whose hinder portion is overlapped by the upper flange of the ectopterygoid (36). The deepest point of the concavity is 9 mm. beneath the straight line joining the apex and the external margin of the lower autopalatine limb. The upper outer surface is inclined at an angle of approximately 125° from the lower. Posteriorly the inner edge of the autopalatine does not follow the curve of the outer edge, but forms an angle by the broadening of the bone towards the lower hinder inner angle. Thus the upper limb of the posterior face of the autopalatine is a triangle with the apical angle very acute, with width of base 8 mm. and height 27 mm., the bone at the apex being 2 mm. in thickness. From the hinder inner corner the outer lower portion of the hind limb of the autopalatine passes outwards beneath the ectopterygoid (36). Thus whereas the outer face of the autopalatine is curved transversely, the hinder face is obtusely angular in cross-section with the inner inferior apex as a longitudinal ridge along the inner base of the whole structure (text-fig. 7).

Anteriorly the lower corner of the autopalatine curves inwards and forwards to form a thick tapering inner basal flange, which is an inward extension of the ridge from the posterior margin. The hinder inner edge of this flange articulates with the outer anterior apex of the parasphenoid (52), just where the vertical process of the parasphenoid originates. This basal projecting portion of the autopalatine is overlapped by the outer

margin of the base of the ectethmoid (38). The transverse section of the anterior portion of the autopalatine is shown in text-fig. 7.

Apparently firmly adherent to the autopalatine is the third lateral dental plate (37") (Plates XI, XXI, and XXV; text-figs. 7 and 10), in which are inserted two powerful tusks as described under Upper Jaw. The inner face of the autopalatine lies 70 mm. from its antimeres.

ECTOPTYERGOID (36).

(Plates XXI, XXII, XXV, and XXVII; text-figs. 6, 10, 11, and 16.)

The ectopterygoid is comparatively long and slender and runs external to the outer lower flange of the anterior limb of the pterygoid (33). It is connected thereto inferiorly by skin, medio-superiorly by cartilage for the greatest part of its length. It originates 47 mm. in advance of the anterior margin of the quadrate, exactly opposite to the anterior edge of the upper limb of the coronoid (41), and 20 mm. internally from that point. The total length of the ectopterygoid is 90 mm. and its greatest breadth is 10 mm. Its upper surface is in shape a triangle with very obtuse apical angle, 1.4 times farther from the posterior than from the anterior corner. The ectopterygoid is joined to the pterygoid for 57 mm. of its length, the actual cartilaginous union ending 21 mm. behind the anterior apex of the pterygoidal flange. The apex of the upper flange of the ectopterygoid just overlaps the outer edge of the pterygoid. From there the inner edge of the ectopterygoid curves gently forward as a very fine lamina overlapping and attached to the hinder part of the outer lower limb of the autopalatine (37) for 20 mm. of its length.

In transverse section the ectopterygoid is U-shaped, with a much thickened base and rapidly tapering apically pointed limbs. Along the lateral margin (apex of curve of the U) the ectopterygoid is superiorly convex in outline. From above, the marginal outline of the structure is slightly sinuous, with concavity opposite the apex of the broadest portion.

The ectopterygoid is apparently the only bone in which large teeth are implanted directly (see Upper Jaw).

ECTETHMOID (38).

(Plates XVII, XXI, XXII, XXV, and XXVII; text-figs. 6, 7, and 11.)

This ossification lies just beyond the ethmoid region, anterior and joined to the palato-quadrate limb. I had earlier (*Nature*, 1939, vol. cxliii, p. 455) stated this bone to be a prevomer. Later investigation has revealed its true nature as an ectethmoidal ossification.

Internally the structure is but lightly ossified, rather cancellate, while the surface laminae are dense. It is composed of a fan-shaped base which is set in the antero-lateral margin of the upper jaw, with the angle of the fan lateral, adjacent to the anterior corner of the autopalatine (37). On the posterior margin of the base there rises from within, curving laterally upwards, a subvertical flange. From the outer (hinder) angle of the base there arises an inverted pyramidal column which meets and overlaps the flange from the hinder edge of the base. This column is set at an angle of about 60° to the plane of the base, and lies in the same plane as the posterior flange to which it is fused and over which it lies. The column thus forms the upper lateral margin of this posterior flange.

In the front of the column, near the base, is a notch in which rests the small base of the rostro-nasal (18). Higher up the column is a facet against which the hind margin of the lateral limb of the rostro-nasal rests.

The greatest length of the base is: below 37 mm., above 33 mm., the difference being the width of the posterior flange. The maximum width of the base is 30 mm., and it is 4 mm. in average thickness. The length of the side of the base along the base of the columnar process is 32 mm. externally and 26 mm. internally. The columnar process is about 34 mm. in oblique length. The highest point of the column is 21 mm. above the upper surface of the base. At the apex, the outer face of the columnar process is 12 mm. in width, somewhat narrower at the base.

The ectethmoid is separated by the least distance of 20 mm. from its antimeres. It rests upon, and is firmly bound to, the inner anterior foot of the autopalatine (37), covers entirely the prevomer (53), and overlaps the anterior outer portion of the parasphenoid (52). The inner curved margin of the base rests against the slight ridge which forms one margin of the wide and shallow central trough in the upper surface of the parasphenoid (Plate XXVII).

The upper face of the dorsal flange of the ectethmoid, including the triangular dorsal face of the pyramidal process, is joined to the flange of the anterior chondrocranium. The outer margin of the hinder face of the pyramidal process of the ectethmoid is firmly bound by tissue to the anterior face of the autopalatine (37). The foot of the lateral rostro-nasal (18) rests in, and is firmly bound by tissue to, a notch at the base of the columnar process of 38, and the main body of the bone (18) lies so as to close in most of the space between the anterior face of the base and the columnar process of the ectethmoid. This whole structure is the main encasement for the olfactory capsules, providing bony support for floor, anterior, posterior, and lateral walls.

The centre of radiation appears to lie at or about the foot of the columnar process of the ectethmoid.

In so far as I can determine, a complete ectethmoid has not been identified in any Coelacanthid remains. I cannot see any such structure in the figures I have examined. In several cases an impression of the basal portion has been observed.

PREVOMER (53).

(Plate XXVII; text-fig. 7.)

The structure which is here provisionally termed the prevomer is an insignificant, rather indefinite, small, anterior adhesion to the inner face of the inner anterior flange of the autopalatine (37). It is an ossified, roughly oval structure covered with adherent loose tissue, 15 mm. in longitudinal length and 9 mm. in width. Its inner posterior margin almost articulates with the anterior trenchant edge of the parasphenoid wing (52). The upper surface of this structure is completely covered by the base of the ectethmoid (38). Very firmly attached to this prevomer is the dermal plate (53") described under Upper Jaw.

I have not ventured to remove the autopalatine-prevomer structure. The general appearance and inseparable mobility of the two apparent sections render it possible that this so-called prevomer may be merely an endo-anterior expansion of the lower anterior flange of the autopalatine (37). An irregular groove between the autopalatine (37) and the prevomer is obvious, and it is possible that they are two separate structures. Between the prevomer and the mid-line, *i.e.* anterior to the parasphenoid (52) and above the postrostral plate (91), there is no ossified structure other than the roofing lower surface of the ectethmoid (38), which does not meet its antimeric across the palate.

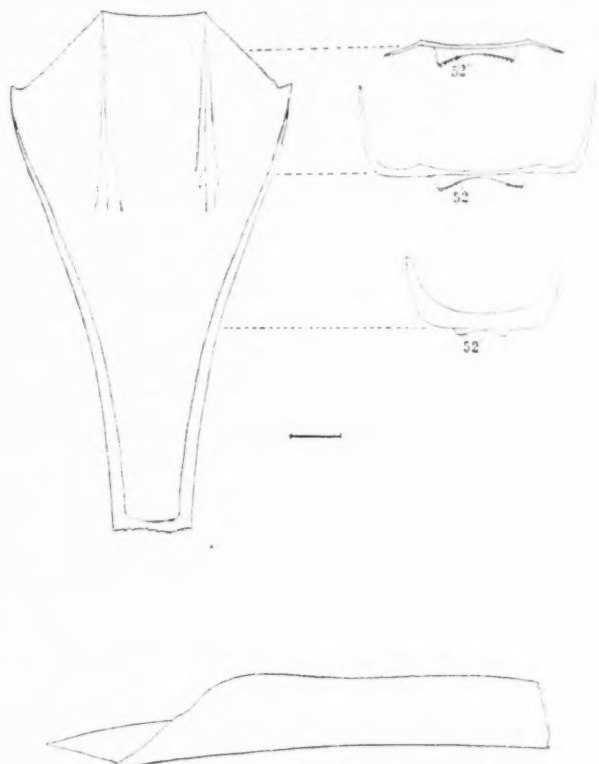
PARASPHENOID (52).

(Plate XXVII; text-figs. 7, 10, 12, 15, and 16.)

The parasphenoid is an unexpectedly massive structure, but is unfortunately incomplete, the hinder portion having been removed by the taxidermist. It originates 23 mm. from the tip of the rostrum, the portion remaining being 100 mm. in length.

In shape the parasphenoid resembles a grocer's scoop, tapering posteriorly to the narrower shank. The shape may be understood by reference to text-fig. 12. Anteriorly the parasphenoid is lamino-radiate in structure, the hinder thicker portion being still densely ossified but somewhat cancellate. The lateral vertical process is anteriorly very thin, but becomes increasingly thicker posteriorly. The anterior point of the parasphenoid is on each side the termination of a longitudinal ridge, which extends approximately 40 mm. along the upper surface. Between these ridges

the bone is gently concave, forming a shallow trough. The portion of the chondro-cranium which remains has for its base the trough of the hinder part of the parasphenoid, and this anterior shallower trough of the bone.



TEXT-FIG. 12.—*Latimeria chalumnae* Smith. Parasphenoid (incomplete) $\times 0.75$.

Above : dorsal view, with position of anterior edge of dentate plate (52") shown by the curved dotted line.

On right : transverse sections at points shown by interrupted lines.

Below : lateral view.

The lateral anterior wing of the parasphenoid is covered by the base of the ectethmoid (38), which fits closely to the surface. The inner margin of the ectethmoid extends to the apex of the small anterior superficial ridge, and covers the parasphenoid inwardly for 15 mm. of its width. It is difficult to determine the centre of radiation of the parasphenoid, but it appears to lie in the base of the trough approximately 80 mm. from the

anterior margin. I am unable to determine whether there is any cavity between the parasphenoid and its dermal plate (52"). The latter originates 5-6 mm. behind the front margin of the parasphenoid (text-fig. 12). The dermal plate is described under Upper Jaw. It appears to be very firmly attached.

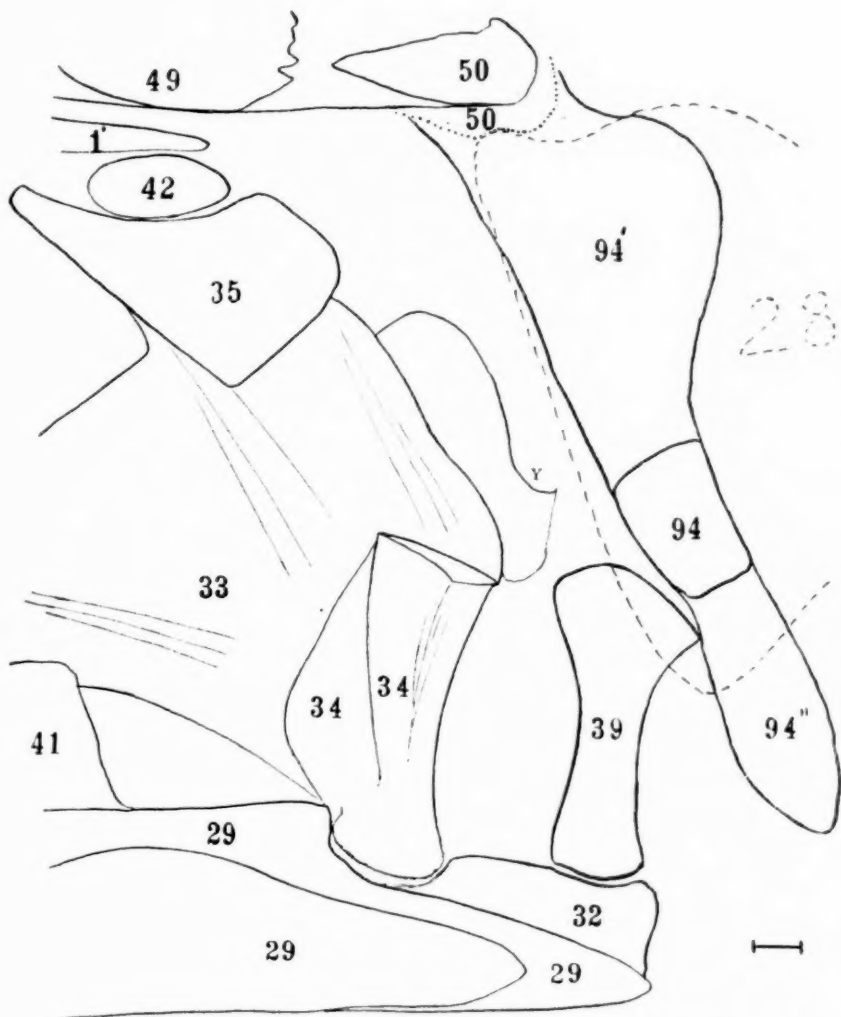
HYOMANDIBULAR (94).

(Plate XXX; text-fig. 13.)

The structure here termed the hyomandibular is a typical cartilage plus median ossification complex, extending obliquely downwards and backwards from the operculo-supratemporal articulation, along the inner face of the anterior margin of the opercular and below. It is very firmly bound to the inner face of the opercular (28) and to the supratemporal (50), and midway along its length to the upper face of the symplectic (39) (text-fig. 13). The structure is approximately 150 mm. in total length and of average width 20 mm. The lower section (94") consists of cartilage approximately 8 mm. in thickness, and is 55 mm. in height. The median portion (94) of the structure is ossified. It is 30 mm. in height, 21 mm. in width; inferiorly 14 mm., superiorly 11 mm., in thickness. The bony walls are fairly thin, and it is either hollow or cancello-porous within. It appears to be merely a bony capsule.

Superiorly (94') the structure for 65 mm. consists of cartilage approximately 7 mm. in thickness, and is expanded to an overall width of about 50 mm., the upper anterior edge being immediately beneath and overlapping inside the operculo-supratemporal articulation. The opercular (28) is firmly held by this structure.

The inner face of the hyomandibular from the lowest portion of the ossified capsule is covered by thin but tough skin, whose upper surface is covered by marginally articulating subrhombic scale-like dentate plates. The posterior plates are small with feeble dentition, whereas a vertical row of five along the inner anterior margin of the ossification are large, and bear three to five graduated sharp spines. The centre plate is 9 mm. in height and 5 mm. in width. The posterior margin of each plate is composed of numerous graduated close-set acute denticles, and the anterior margin bears five antrorse spines of which the centre is the largest, 5 mm. in length. This squamation extends up above and forward of the symplectic (39), and the skin there forms a lobate marginally thickened fold (Y) (Plates XXI, XXV, and XXVIII), which possibly formed or covered the hinder edge of the hyoidean gill slit (H). Externally these articulating scale-like plates gradually diminish in size and spination posteriorly and superiorly on the skin. The spines are in every respect identical in structure with the teeth of the rostral plates (*q.v.*). They are generally more



TEXT-FIG. 13.—*Latimeria chalumnae* Smith. Left side of head with outer skin and dermal cheek-bones removed, showing hyomandibular. The opercular is shown by interrupted outline. The line represents 1 cm. For explanation see Folder-page I at end.

slender and apically more heavily enamelled, and the pulp cavity is not as large, but extends almost to the apex.

The structure identified in *Wimania sinuosa* Stensiö by Stensiö (Stensiö, Triassic Fishes, Spitzbergen, 1921, p. 74) as an epiphyal I am inclined to consider represents the medial capsular ossification of an hyomandibular system, which would lie in the position described, i.e. postero-medially of the pterygoid.

SYMPLECTIC (39).

(Plate XXX; text-fig. 13.)

In a brief note to Nature (1939, vol. cxliii, No. 3627, p. 749) I stated that an epiphyal and a ceratohyal were present in this specimen. I had not at that time ventured to explore within the skin above the inner side of the articular (32), and considered the structure now termed symplectic to have been the upper limb of the ceratohyal.

This symplectic is 65 mm. in height, with shank of elliptical cross-section 11 mm. in width at narrowest part, which occurs about midway along its length. Both ends are dilated, the lower along both axes of the ellipse, and the upper along the major axis, with some decrease along the minor (text-fig. 13). The lower condyle articulates with a facet on the dorsal surface of the hinder portion of the articular (32), the joint being firmly enveloped in cartilage.

The upper end spreads more or less fanwise, posteriorly exaggerated so as to give a projecting lobe. The outer surface of the symplectic is firmly attached to the inner surface of the thick preopercular flap, and is firmly bound thereto by a covering of extremely tough skin. The upper edge of the superior dilation is firmly attached by cartilage to the anterior face of the hyomandibular complex (94), the ossified lower corner of that structure almost touching the hinder upper edge of the bone of the symplectic. The outer face of the end of the hinder lobe of the symplectic is firmly bound to the inner face of the lower corner of the opercular (28). There is no point at any portion of the inner surface of this symplectic where a ceratohyal could have articulated. The investing skin was complete and covered the whole surface.

In pl. iv, fig. 2 (Stensiö, Triassic Fishes, Spitzbergen, 1921), there shows in *Wimania sinuosa* Stensiö a bone labelled by Stensiö "y," and described by him in the legend as "y, loose bone probably from the shoulder girdle." That bone I consider to be identical with that here described as a symplectic. It has been disturbed hardly at all from the position it should have as deduced from what I have seen in *Latimeria chalumnae*, i.e. it lies almost parallel with and just posterior to the quadrate, its lower

end articulating with the upper surface of the articular, and the dilated head partly behind the opercular.

In pl. xi (*ibid.*) of *Azelia robusta* Stensiö (specimen P. 195), Stensiö labels a fragment of bone "*Br*," designated in the legend as portion of a ceratobranchial. This may be part of the symplectic.

This bone may legitimately be termed symplectic despite the fact that it does not unite the hyomandibular directly with the quadrate. It is possible that the system in this fish is the typically primitive relationship between the pterygoid and the hyomandibular arches. The hyomandibular system in *Polypterus* suggests that the hyomandibular itself of those fishes has been formed by fusion of the elements here termed hyomandibular (94) and symplectic (39). The system in *Amia* is not widely divergent, while those of existing Chondrostei show marked similarity in structure and function to that described in *Latimeria*. (This in so far as I am able to deduce from diagrams, not having any material for dissection.)

THE FRONTO-INTERTEMPORAL JOINT AND ITS STRUCTURAL RELATIONSHIPS.

In Coelacanthid remains the head often appears to have broken transversely between the frontals and the intertemporals. It has been generally accepted that some form of joint in, or division of, the skull occurred at that part. In the light of what has now been learned, this transverse cleft has probably been somewhat exaggerated in most reconstructions. It had been supposed that there was some degree of flexion between the anterior and the post-frontal parts of the head. My observations incline me to the view that the Coelacanth head possesses rigidity in greater degree than has been supposed, but that there is quite probably some degree of independence of movement between the anterior and the posterior parts. A slight degree of flexibility might assist in the firm locking of the jaws if strong jaw muscles are present, which appears to be the case in this specimen.

This characteristic fronto-intertemporal joint is clearly marked in this specimen, its course being visible as a depression in the shrunken skin posterior to the exposed parts of the frontals. The intertemporals (49) are firmly sutured along the mid-line of the head, while the frontals are rather loosely articulated with one another. The posterior edge of the main lamina of the frontal is somewhat irregularly bevelled downwards. This produces a narrow V-shaped gap between the hind margin of the frontal and the anterior margin of the intertemporal, the lower edges more or less articulating and bound together by tissue below. The roof

of the chondrocranium is firmly bound to the lower surfaces of the bones. There is no cartilage or other tissue between the frontals and the intertemporals in the trough of the joint. Superiorly, over the trough the two bones are united by the thick skin of the head, which is firmly anchored to the base of the exposed portion of the bones composing the joint. In so far some degree of flexibility may be expected in such a structure. The whole is, however, continued posteriorly by the infero-posterior process of the frontal, the alisphenoid (1'). This projects obliquely backwards beneath and almost parallel with the ventral surface of the intertemporal, to which it is firmly bound by tissue. At the same time it overlaps the antotic process (42) of the basisphenoid, to which it is as firmly bound, the latter in turn being fixed to the upper surface of the metapterygoid (35) between the ascending and the antotic processes of that bone. Internally the inner edge of the alisphenoid is almost certainly invested by the cranial cartilage. The frontal (1) is thus firmly bound to the intertemporal (49) and becomes an integral part of the pterygo-quadrato system. The whole of the forepart of the head is therefore united with the posterior limits of the pterygoid system in such a manner as to produce a strong and fairly rigid structure.

Via the ramus of the lower jaw, the hyomandibular system is connected with the quadrato-ptyergoid column. The opercular (28), in virtue of its relation to the hyomandibular (*q.v.*), is functionally also an integral part of that system.

The postfrontal, *i.e.* intertemporal-supratemporal, region of the skull, is to some extent a separate entity. It is almost merely a roofing, albeit massive, structure, anchored by the ventral surface anteriorly to the quadrato-ptyergo-frontal, and posteriorly to the operculo-hyomandibular systems, thereby linking those structures dorsally.

The base of the cranium, chiefly through the antotic processes of the basisphenoid, is at least in part dependent upon suspension from the pterygoid columns. The sphenoidal structure provides additional strength and rigidity to the main skeletal system, since it restricts or prevents any lateral movement of the pterygo-quadrato columns.

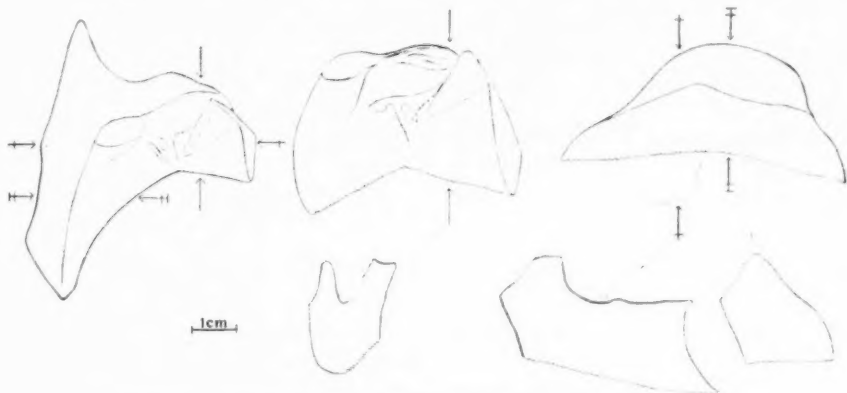
PROTIC (93).

(Plates XXI and XXVIII; text-figs. 11, 14, 17, and 18.)

Only the dorso-lateral portion of this structure remains, the rest having been sliced away by the taxidermist. The portion remaining has an inner face which lies in the lateral wall of the brain cavity. This face is approximately 63 mm. in length and 27 mm. in height, and it lies almost parallel with the sagittal axis. Outside this process is a large semi-compressed

columnar projection which lies over somewhat towards the inside, thus presenting a lateral surface which faces upwards and outwards. In external appearance this structure is somewhat spindle-like, the anterior limb being the lateral basal structure of the inner face, and the posterior limb the columnar projection previously described.

Along the upper edge of the inner face the prootic is attached by firm cartilaginous tissue to the inner inferior margin of the intertemporal (49),



TEXT-FIG. 14.—*Latimeria chalumnae* Smith. Remaining portion of prootic (93).

Top left: View from above.

Top centre: Lateral view, much as position shown in Plate XXVIII.

Top right: View of inner face which forms part of the lateral wall of the brain cavity.

Articulation facet for supratemporal infero-antrorse process (50') dotted.

Below: Cross-sections, taken as shown by plain, one-barred, and two-barred arrows. Jagged edges show where portions of the structure had been removed.

the whole apparently having formed part of the lateral wall of the neurocranial cavity. The upper inner edge of the postero-exterior columnar limb appeared to have been attached by cartilage to the inner lower ridge of the supratemporals (50). Unfortunately this part had been so mutilated that I can give little information about it. On the upper hinder margin of the lateral face of the posterior columnar process is the triangular facet for reception of the laminate infero-antrorse process (50') of the supratemporal. Slightly anterior and below the apex of this facet, the face of the bone is moulded to receive the covering ossicle (92), which, by envelopment of the base within stout tissue, is firmly bound to this outer limb of the prootic, serving to bind the supratemporal process also.

It is exceedingly difficult to describe this structure adequately, but various views and sections are shown in text-fig. 14.

In the dorsal portion of the posterior columnar limb is a deep channel

filled with the cartilage which spreads over the outer hinder face of the column, and which is attached superiorly to the supratemporal (50). A canal 2-3 mm. in diameter runs through this cartilage, which probably carried branches of nerves V and VII, but I am not prepared to be definite on this point. At any rate, these nerves appear to have run forward and downward along the outer face of the prootic after emerging from the groove. There is a deep excavation in the lateral face of the anterior limb, but I cannot be certain whether it is artificial or not, though it appears not to be natural.

The whole prootic is extremely light and cancellate in structure. The inner face bears an angular median, fairly sharp longitudinal ridge. Most of the anterior limb of the structure lies within and behind the metapterygoid (35). The posterior limb, with the covering ossicle, becomes visible externally when the postorbital (23) and the squamosal (24) are removed.

PROOTIC OSSICLE (92).

(Plates XXI and XXVIII; text-fig. 11.)

Over the end of the supratemporal process, and overlapping it, is a small capsular ossification of peculiar structure (92), which is firmly bound to the lateral face of the prootic (93) by strong tissue. This structure binds the supratemporal limb (50') very firmly to the prootic (93) also, since the pointed apex of the former lies in a slight moulded fossa in the face of the prootic. This external structure I name provisionally "prootic ossicle." In so far as I can determine it serves chiefly as a binding element, possibly also as a form of protection for the branches of the V and VII nerves, which appear to run along the lateral face of the prootic (*q.v.*).

This ossicle (Plate XXVIII) is merely a capsule of very light structure. It consists of a basal plate, roughly tri-equilateral, of side 16 mm., which rests against the lateral vertical face of the prootic. From the lateral (outer) face of the base of the ossicle arises a hollow structure which turns immediately downwards and dilates inferiorly, chiefly posteriorly, into a lobe 17 mm. in length and 7 mm. in height. This lobe hangs over and not far beyond the margin of the lower portion of the base, with its outer face about 7 mm. outward from the base. This lower lobe thus projects downwards as a flange over the lower outer face of the prootic.

In contrast with the smooth surfaces of the supratemporal inferior limb (50') and of the outer face of the prootic (93), the surface of this ossicle (92) is reticulately rugose and striate. The surface ridges may be covered with ganoin. The prootic articulation with and without the ossicle (92) is figured in Plate XXVIII. The form of the structure on the prootic suggests a small external "ear." Actually the whole supra-

temporal-prootic articulation complex is not visible externally, being covered by the hind margin of the preopercular system. It is connected with the outside by the external opening of the antotic cavity (V) on the outer face of whose inner wall it lies. This antotic cavity opens behind the "preopercular system" (hind limbs of postorbital (23), squamosal (24), and preopercular (25)).

So light is this ossicle that it would probably not often remain with the heavier structures during decomposition, and would probably not often be seen with fossil remains. I am inclined to consider that it shows in a figure (Stensiö, *Triassic Fishes*, Spitzbergen, 1921, pl. xi) of *Arelia robusta* Stensiö labelled "Pro-o.," described in the legend as "Only a postero-lateral part of the prootico-opisthotic." It appears from the figure that the ossicle has suffered an anticlockwise twist through about 90°, the hinder part of the outer lobe thus pointing upwards. In pl. xiii (*ibid.*) the impression of the base of this ossicle is probably indicated by "Pro-o."

CHONDROCRANIUM.

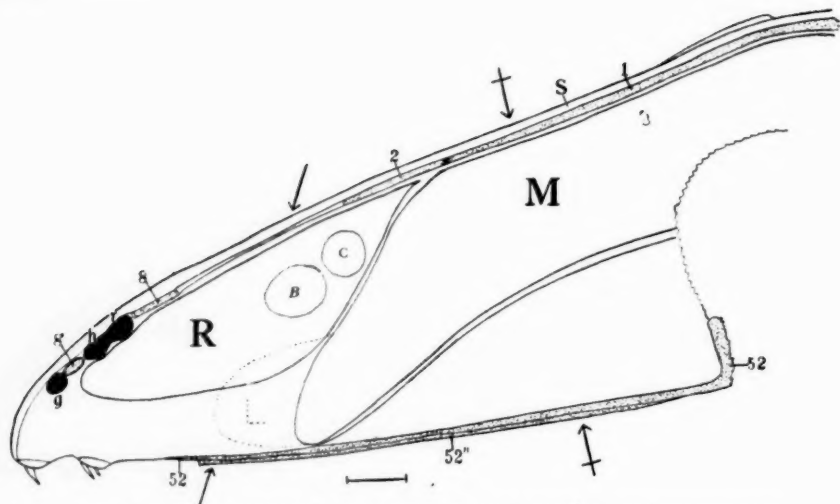
(Plates XXI, XXII, XXV, and XXVII;
text-figs. 6, 7, 11, 15, 16, 17, and 18.)

This structure was somewhat hacked about during mounting. Anterior to the intertemporals (49), the central portion at least appears to be complete. The posterior portion has only the upper and upper lateral portions. It is almost impossible to trace the origins and exits of the cranial nerves from what remains. Only the course of the ophthalmic branches of the V and VII nerves has been found. Even anterior to the intertemporals, the median portion, *i.e.* the posterior flange from the interorbital septum, has been cut away. The remaining portion of the anterior part of the chondrocranium is in transverse section almost triangular, resting on a blunted apex in the trough of the parasphenoid (52), which widens anteriorly. This is shown in text-figs. 7, 15, and 16.

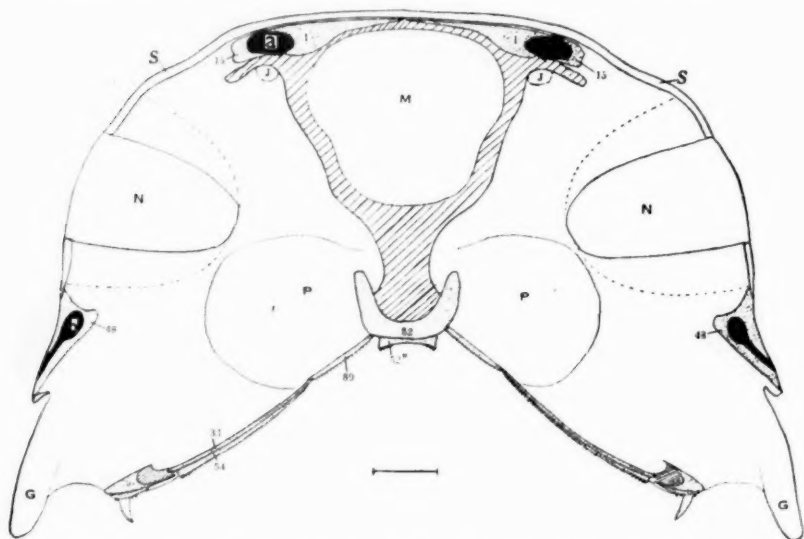
The upper surface of the anterior part of the chondrocranium is gently convex, the fronto-rostral series of bones resting upon and fixed to it. This surface spreads laterally to form a narrow flange curving over the orbital and nasal structures. Anteriorly the flange is joined to the top of the columnar process of the ectethmoid (38), posteriorly to the metapterygoid (35).

Adjacent to the basal portion of the chondrocranium in the parasphenoidal groove were the remains of a relatively large muscle sheath (P), probably for the anterior muscles of the eye.

From the foramen (J) in the alisphenoid (1') the dorsal branches of the V and VII nerves pass into a tube in the lateral flange of the chondro-



TEXT-FIG. 15.—*Latimeria chalumnae* Smith. Sagittal section of anterior neurocranium. Sensory canals heavy black. Bone sections dotted. The anterior plain arrows show the position of the transverse section figured in text-fig. 7, the barred arrows that figured in text-fig. 16. The line represents 1 cm. For explanation see Folder-page 1 at end.



TEXT-FIG. 16.—*Latimeria chalumnae* Smith. Transverse section of head 100 mm. from snout tip (see text-fig. 15). Cartilage shown by parallel line shading. Sensory canals black. Bone sections dotted. The line represents 1 cm. For explanation see Folder-page 1 at end.

cranium. This continues forwards for about 20 mm. and then emerges to run beneath the flange. Finally the nerve channel again pierces the flange to open into the upper lateral narial tube (C), thence to the lower lateral narial tube (B), and finally to or over the olfactory capsule (E) also. (See Olfactory Organs.)

In the anterior part of the chondrocranium lies the large ethmoidal cavity (R) (*q.v.* under Olfactory Organs). Beneath this lie the olfactory lobes (L) of the fore-brain (text-figs. 7 and 15). Antero-laterally to these are the olfactory capsules (E) bounded postero-laterally by the ectethmoid (38).

BRAIN CAVITY (M).

The brain in this specimen shows a typical primitive anterior prolongation. The roof of the brain cavity sweeps as unbroken cartilage from the hind margin of the intertemporals (49) forwards to the rostrum. The fore-brain is of moderate diameter, and the tubular cavity dips downwards in the anterior chondrocranium to run beneath the rostral sinus (R). The brain divides below the hind margin of that sinus. There is a small double depression on the lateral walls of the anterior brain cavity, but it is not a foramen (text-fig. 15). In the apex of the cavity for the olfactory lobe there is a foramen for the entry of nerve I to the olfactory capsule (E).

The interorbital septum is fairly thick (and entirely cartilaginous). Little can be said about the posterior portion of the chondrocranium, since most of it had been removed, and I did not dissect that region of the roof of the neurocranium. As has been mentioned, the chondrocranial ossifications, excepting a portion of the prootic (*q.v.*) and the apex of the antotic process of the basisphenoid, have been removed.

In text-figs. 17 and 18 the probable size of the brain cavity posterior to the frontals has been indicated.

BASISPHENOID (96).

All that remains of the basisphenoid is the lateral extremity of the antotic process (42). Judging from this, the basisphenoid itself was but lightly ossified and highly poro-cancellate in structure.

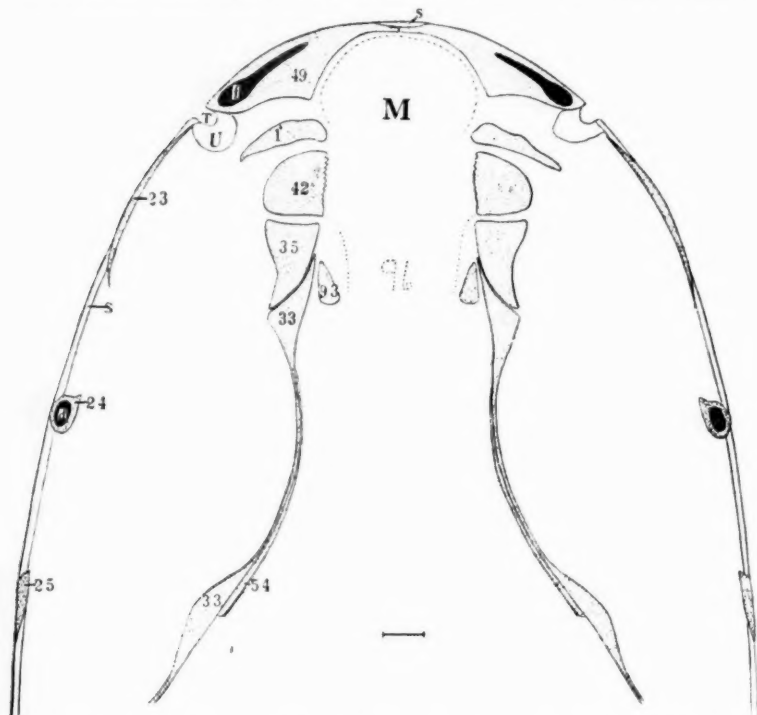
The remains of the antotic process (42) had been sliced into three parts during the mounting. The outer convex face was in position on the metapterygoid (35) with an inner slice hanging by a thread, while the third part was found in the straw with which the cranium was stuffed. The three parts fit to form a nodule which represents the lateral horizontal limb, the antotic process, of the basisphenoid. The limb is 8 mm. in depth, the nodular apex about 23 mm. in length, and faced with stout

cartilaginous tissue. It was firmly attached to the dorsal surface of the metapterygoid (35), and to the ventral face of the alisphenoid (1').

RESPIRATORY ORGANS.

(Plates X, XI, XII, XIV, and XV.)

Spiracle (F).—The spiracles are small and situated at the anterior end of a shallow lateral spiracular groove (T). Since all the tissues beneath

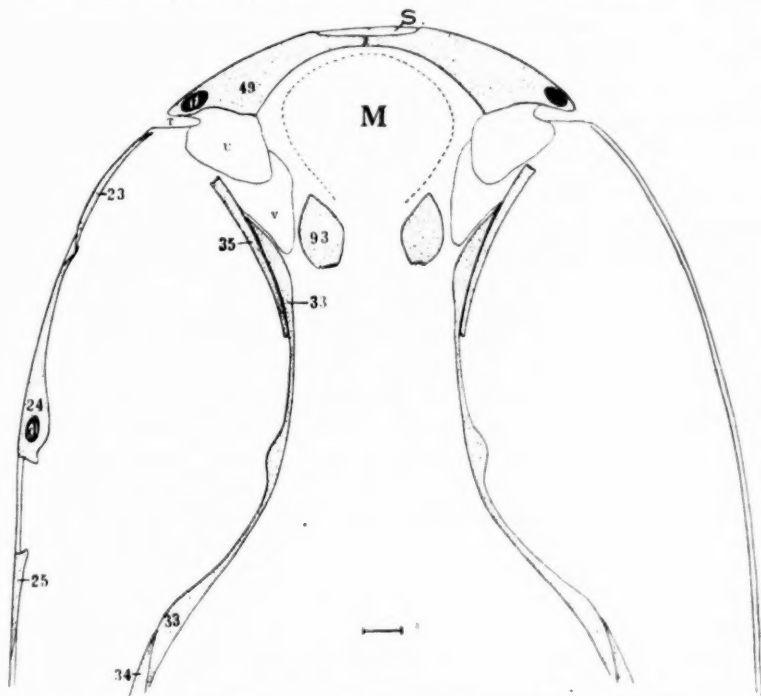


TEXT-FIG. 17.—*Latimeria chalumnae* Smith. Transverse cross-section of head about 165 mm. from snout, indicated by plain arrow in text-fig. 11. The dotted lines indicate the possible basisphenoid in section. The interrupted lines outline the probable brain cavity. The line represents 1 cm. For explanation see Folder-page I at end.

the skin had been torn away, it is not possible to give any information about the course and nature of the spiracular tube. There is a posterior, here named spiracular pouch (U), which is described below. Its connection with the spiracle is not certain. The spiracles are probably functionless.

Gills.—Every part of the gills had been removed from this fish, and discarded, save only the copula (45, *q.v.*).

Chiefly from what I find on that organ, it seems almost certain that there were only four gill-arches. *Wimania* Stensiö and *Axelia* Stensiö



TEXT-FIG. 18.—*Latimeria chalumnae* Smith. Transverse slightly oblique section of head 185 mm. from tip of snout, indicated by crossed arrow in text-fig. 11. The brain cavity is approximate only. Bone sections dotted. The line represents 1 cm. For explanation see Folder-page I at end.

are stated to have had five. It is possible that some other structure, *e.g.* symplectic, may have been mistaken for part of a gill-arch, and that the number is constantly four.

The arches were apparently in part cartilaginous, united to the lower surface of the copula and also to some median basibranchial, whose head articulated with a facet in the hind face of the capsular basihyal ossification (100). The gill-arches are stated to have been spinate. I presume that they bore structures resembling the dentate plates occurring on the inner face of the hyomandibular (94, *q.v.*).

The gill-filaments are stated to have been "Like the ordinary gills of a fish, and reddish in colour." I cannot give any further information.

The articular-symplectic-hyomandibular system in this fish is so arranged as to make it likely that the opening of the mouth would relax the gill-cover. That is, the opercular (28), an integral part of the hyomandibular, would tend to open outwards as the post-quadrate portion of the lower jaw moved upwards. I cannot find any evidence of other muscular or tendinal control of the opercular membrane. It appears as if the opercular itself must play an important part in the control of the degree of opening of the gill-cover.

SPIRACULAR POUCH (U).

(Text-figs. 11, 17, and 18.)

Lateral to the apex of the antotic cavity (V) lies a pouch enclosed by membrane bordering the hinder margin of the processus oticus of the metapterygoid (35). This pouch lies completely ventral to the intertemporal (49), its roof being adherent to the face of the inner inferior ridge of that bone. The hinder portion of the outer face of the pouch is covered by the postspiracular (51). The structure was damaged, but appears to have had no external opening excepting possibly anteriorly into the spiracular canal.

The pouch is 37 mm. in length, about 18 mm. maximum depth, and approximately 14 mm. transverse width. The membranous lining of the cavity is rather delicate, and though it shows no trace of being vascular, its condition does not permit of any definite opinion on that matter.

The structure probably represents a saccular diverticulum of the spiracular tube, but it would be venturesome to express any definite opinion about it, since no connection between the two could be determined with certainty. A dorsal "pouch-gill" as an adjunct to the ordinary structure of a spiracle may conceivably have been developed in some early forms, possibly of greater function than the diverticula found in some living forms. This species has so obviously retained primitive characters but little modified, if at all, that many structures found upon it will repay most detailed investigation when a complete specimen is found.

ANTOTIC CAVITY (V).

(Text-figs. 11 and 18.)

From the inner anterior surface of the opercular membrane there extends upwards and inwards a thick heavy membrane which, in thinner

form, covers the outer face of the prootic (93), and which is connected by its lower edge to the hinder face of the metapterygoid (35). It sweeps upwards to slightly in advance of the processus oticus of the metapterygoid, ending just above the antotic process of the basisphenoid (42) as a blind conical sac. The upper wall is attached to the inner ridge of the lower surface of the intertemporal (49) (text-fig. 18). It is thus extracranial, but within the pterygoid column.

The outer apical membrane is the inner wall of the spiracular pouch (U). The hinder lower portion of the membrane, where it originates against the anterior opercular margin, is adnate to the thick cartilaginous upper section of the hyomandibular (94') which connects the opercular (28) with the hinder outer angle of the supratemporal (50).

The lower portion of the membrane forms a rounded, vertically elongate lobe (Y) (Plates XXI, XXV, XXVIII, and XXX), much thickened and strongly dentate. Quite possibly this formed the posterior border of the presumed hyoidean gill-slit (H). The outer anterior and hinder face of the lobe bears small marginally articulating dermal plates, which are obviously modified scales, either quadrangular or rhombic. The upper outer plates bear one or two minute spines. Those on the lower anterior and inner face of the lobe bear large, slightly curved spines, mostly with an encirclement of smaller basal spines.

POSTSPIRACULAR GROOVE (T).

(Plates X, XI, XII, XIV, XV, XVII, XXI, and XXVIII;
text-figs. 11, 17, and 18.)

From behind the spiracle below the anterior third of the intertemporal (49) runs a narrow groove or trench, the trough of which is composed of fairly thick tissue, the lower portion being the roof of the spiracular pouch (U). The upper margin is formed by the lower lateral edge of the intertemporal (49) and the supratemporal (50), the lower margin by the upper edge of the postorbital (23). The hinder end of the skin of the groove overlaps the antero-inferior flange of the postspiracular (51).

SQUAMATION.

(Plates XXX, XXXIII, XXXIV, XXXV, XXXVI, XXXVII,
XXXVIII, XXXIX, XL, XLI, XLII, and XLIII;
text-figs. 2, 19, and 20.)

The body is completely scaly. Only the first dorsal and the apical portions of all fin rays are naked. On the lobed fins the scales completely cover the penduncles and widen apically to form a lobe.

There are no normal scales on the head (but see Subopercular, Inter-

opercular, and Postspiracular). The anterior margin of the hinder edge of the presumed hyoidean gill-slit (H) bears articulating scale-like structures (*q.v.*). On the nape the scaling extends forwards and ends immediately behind the commissural of the supratemporal canal (*t*), and thus has an undulate margin. The two most anterior extremities of the scales are on each side 93 mm. behind the anterior margin of the intertemporals (49). On the mid-line the scales end immediately behind the inter-extrascapular (55) (text-fig. 2).

The scales are cycloid, and the whole surface is very finely corrugated with transversely striated ridges. The exposed portion of the scales is mostly covered with elongated tubercles, either rounded or posteriorly apically pointed, like spines. The scales are comparatively thick, but noticeably softer than those of ordinary teleostean fishes. They are comparatively lightly ossified. Alizarin staining and clearing of the scales is almost impossible without deformation, since they swell and partially dissolve in alkali. The tubercles also are loosened from the surface by treatment with alkali. Upon ignition of the spirit-dried unornamented portion of a mid-body scale, the residue was only 11.2 per cent. The scale of a juvenile Sparid fish, *Austrosparus auriventris* (Peters), by similar treatment, gave a residue of 32.4 per cent., and scales from a 55-lb. Sparid fish, *Cymatoceps nasutus* (Castlenau), left a residue of 51.4 per cent. In all cases the residue appeared to be chemically identical.

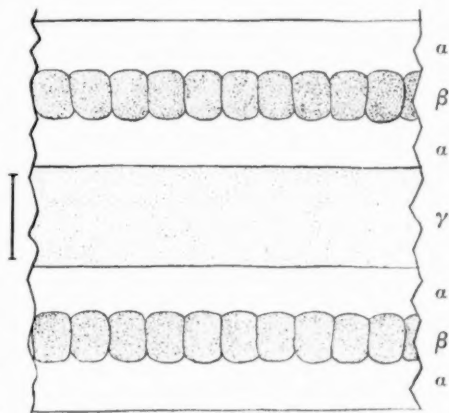
The circuli are comparatively fine, and exhibit some degree of annulation. From this it has appeared that the age of the specimen is possibly somewhere between twenty and twenty-five years. The annulation is of interest in indicating that the species is unlikely to be of bathybial habit.

Each tubercle is set in a more or less oval, very fine laminate basal plate, which fits exactly over the corrugations of the scale surface, the plate itself thus being corrugated. The tubercles are mostly hard and smooth above, but in some cases there appear to be indications of obsolescent blunted granulations along the base. (Tubercles of the extracleithrum, *q.v.*, have a rugose surface.) The basal plate exhibits a moderate degree of birefringence. The tubercles are hollow, the (pulp) cavity extending most of their length, and there is no obvious connection between this cavity and the base of the scale. The body of the tubercle is composed of tissue showing only the faintest trace of radial structure. This tissue shows weak birefringence with undulose extinction suggestive of strain rather than crystalline structure. In one tubercle there shows a patch which remains permanently extinguished on rotation. The outer layer of ganoin is comparatively thin, about 0.08 mm. in thickness.

The unornamented part of the surface of a scale when cleaned with

chloroform rubs into a mass of thread-like tissue. In transverse section the body of a scale is longitudinally striate, composed of layers of three distinct types (α , β , and γ) arranged in regular series. The layer α is about 6μ in thickness and exhibits a mild degree of birefringence with fairly sharp extinction. The interference colour is light yellow. This layer appears to be uniform in structure. The layer β is about as thick as α , but is cellular and almost isotropic. The individual cells are about $4.5\mu \times 6\mu$. The layer γ is about 12μ in thickness, very weakly birefringent, of blue interference colour, and apparently uniform in structure. The three layers appear to be uniformly arranged as follows: $\alpha\beta\alpha\gamma\alpha\beta\alpha\gamma \dots$ throughout the thickness of the scale. The upper series of layers are graduated slightly thicker than those below. The weak birefringence exhibited is probably due to strain rather than to crystalline structure.

The scales possibly represent an advanced stage of modification of the primitive cosmoid type, in which the cancellate bone-layer has disappeared, with consequent reduction in the thickness of the scale. That the ancestral form bore true cosmoid scales is very probable (see Tooth-plates above).



TEXT-FIG. 19.—*Latimeria chalumnae* Smith. To show the arrangement of the layers and their appearance between crossed Nicols in a transverse section of the body of a scale. From a scale 0.6 mm. in thickness. The line represents 10μ .

SCALE COUNTS, ETC.

Lateral line 76, + 23 on the supplementary caudal, *i.e.* total 99.

23 predorsal scales from origin of scaling on nape to origin of first dorsal, 39 to origin of second dorsal, and 59 to origin of principal dorsal caudal rays. 6 scales along base of spinous dorsal, 8 from end of base of first dorsal rays to end of dorsal membrane, 6 from end of membrane to origin of second dorsal. 22 scales round the base of the peduncle of the second dorsal, 22-23 scales from the back along the anterior face of the second dorsal peduncle, 10 across the widest part of the lobe. 18 round

the base of the right pectoral peduncle, 27 from the body along the lateral face of the peduncle, and 12 across the widest part of the lobe. 22 scales round the base of the anal peduncle, 23 from the body along the anterior face of the peduncle, and 8-9 across the lobe. 18 round the base of the peduncle of the left ventral (which is damaged), 17 from the body along the peduncle, and 11 across the widest part of the lobe.

40 scales round the narrowest part of the caudal peduncle, 24 across the body from the origin of the principal dorsal caudal rays to the origin of the principal ventral caudal rays. 7 across the anterior part of the supplementary caudal. There are 5 series of basal scales on the posterior principal dorsal caudal rays.

50 scales round the body just in advance of the first dorsal, and 44 just in advance of the second dorsal. 6 series between the lateral line and the lateral margin of the base of the first dorsal, 7 to the lateral margin of the base of the second dorsal, and 13 from the lateral line to the origin of the principal dorsal caudal. 10 scales from the lateral line to the upper edge of the pelvic base, 9 to the lateral edge of the anal base, and 12 to the origin of the principal ventral caudal. From the pectoral axil to the front margin of the pelvic base there are 15 scales.

The scales are disposed in regular rows which run slightly obliquely downwards and backwards. They are largest in a roughly triangular area whose slightly convex margins run from pelvic to shoulder, and from pelvic to the base of the second dorsal fin. Naturally there is no sharp line of demarcation, but those within that area are almost uniformly large, the largest being broadly oval or even sub-quadrangular, about 50 mm. in length and 40 mm. in width, while the exposed portion of the scale is about one-fourth of the total area, and more or less rhombic (see scale 68, Plate XL).

On the body, the ornamentation on the dorsal scales is heavier and coarser than on those on the ventral surface, there being almost regular gradation in this respect. Practically the whole of the exposed surface of each dorsal scale is covered with tubercles. Ventrally the exposed surface ornamentation diminishes progressively, that of scales of the ventral surface in most cases covering not more than half of the exposed area, and the tubercles are small.

On all parts of the caudal peduncle the ornamentation on the scales is more or less uniform. On the forepart of the body the tubercles are as a rule longitudinally elongate, but vary in shape and direction of elongation, though all have an entirely smooth, gently rounded upper surface. Towards the hinder part of the body the tubercles show an increasing degree of prolongation of the hind margin, until from below the second dorsal fin they are in the form of depressed retrorse spinelets, that part of the

squamation having a coarse appearance and being rough to the touch.

The largest tubercles are found on scales in a roughly semicircular area on the dorsal surface of the body, of which the profile of the back between the two dorsals is the diameter. Nowhere are the nature and arrangement of the tubercles absolutely uniform, even in a comparatively restricted area. In one case, on the right side below the second dorsal, is an area in which the exposed surface of most scales bears 20-25 slightly irregularly caudally radiating rows of moderate tubercles, 3-10 tubercles in each row. In the centre of that area are three adjacent scales whose exposed surface is abruptly different from that of the surrounding scales, in bearing only 20-28 very large tubercles, somewhat irregularly shaped, set at all angles. Also in that same area are other scales on whose exposed surface is anteriorly a group of a few large, irregularly shaped tubercles, while the hinder portion of the ornamentation conforms with that characteristic of the area described.

There is a high degree of variation in size and shape of scales on this fish (as indeed in all fishes). The variations observed in this specimen show clearly how unreliable as even specific characters individual scales or even isolated groups of scales may be. Illustrations of scales from many different parts of the body are given in Plates XXXIII-XLII. The wide variation in size, shape, and ornamentation is clearly shown especially in Plate XLII.

There is generally abrupt differentiation between the scales on the body and those on the lobed fins. In the axil of the pectoral the scales become abruptly smaller than those on the body, and there is one with a distinctly lobate hind margin reminiscent of a rudimentary axillary scaly process (80, Plate XLII). On the limb of the fin the scales become increasingly smaller, and elongated (74 and 81, Plates XXXV and XLII), and at the base of the rays the scales are almost five times as long as wide. On the outer (lateral) face of the lobe and peduncle of the pectoral fin the ornamentation of the scales is comparatively feeble and sparse. On the opposite (inner) surface the scales are comparatively densely ornamented with small close-set spiniform tubercles (the outer lateral surface of the rays bears spines, the inner surface being smooth, the opposite of what is observed on the scales). On the body beneath the pectoral fin, the surface ornamentation of the scales becomes extremely diminished, some scales bearing only a few tubercles about the centre of the exposed area.

In the case of the pelvics the same abrupt change in the squamation is observed. The proximal scales are small, almost quadrangular (82, Plate XLII), but become distally more elongated, those at the base of the rays being elongate-oval (83, Plate XLII).

At the base of the second dorsal there is also a very abrupt change

in shape and size of the scales. On each side of the base are several upright scales whose upper surface is truncate with posterior lobation, and with only small exposed portion, almost marginal, bearing subciliate tubercles (86, Plate XLII).

LATERAL LINE.

The lateral line originates at the upper hinder edge of the exposed portion of the supratemporal (50), the anterior scales with strongly ossified heavy tubes. The lateral line curves gently upwards over the pectoral to within about 60 mm. of the dorsal profile at about the tenth scale. Thereafter it runs slightly downwards in almost a straight line to the fifty-first scale (65) slightly in advance of the anterior dorsal principal caudal rays. Thence the lateral line curves slightly downwards, running immediately beneath the obtuse keel-like longitudinal ridge on the middle of the peduncle. Near the hind end of the peduncle the line curves slightly upwards and continues uninterrupted to the extreme hind margin of the scaling on the supplementary caudal. The tubes of the lateral line scales bifurcate, the bifurcations generally running along the upper and lower margins of the ornamented face. The tubes open outwards by numerous small foramina, generally uniserial, in the upper face of each bifurcation. These small foramina may be seen in figures of the anterior lateral line scales.

LATERAL LINE SCALES.

(Plates XXX, XXXIV, XXXVII, XXXVIII, XLI, and XLII;
text-fig. 20.)

On the left side the first lateral line scale (60, Plate XXX) is a small but massive structure. The exposed portion is 28 mm. in height and 14 mm. maximum width. The overall length is 20 mm. The exposed portion of the scale is about two-thirds of the total surface. The outer (posterior) margin is convex, slightly undulate. The surface is sparsely covered with small rounded to elongate-oval tubercles arranged very regularly as twenty posteriorly radiating rows. The exposed surface is bounded supero-posteriorly and infero-posteriorly by the main branches from the sensory canal. Between these lie near the surface four or five smaller canals, reticulately interconnected. The portion of the scale beneath the skin is almost 7 mm. in thickness medially. Superiorly there is a normal but much abbreviated dermal flange. The hind mid-portion of the scale consists of a bony tubule, of 4 mm. internal diameter at the hinder end, which branches dorso-posteriorly. The lower main branch has numerous perforations proximally. The main tube is contained posteriorly as a solid structure 15 mm. in length, the posterior opening being directed somewhat down-

wards. The hind portion of this canal thus has the appearance of a cup-shaped projection on the lower surface of the scale. This fits closely over an outer foramen in the anterior portion of the second lateral line scale, which is the anterior end of the canal in that scale. On the ventral surface of the sensory tubule is a ventrally directed tubular process with infero-lateral aperture, obviously for innervation within the scale.

The second lateral line scale (79, Plate XLII) is merely a larger edition of the first, but of lighter structure. The outer surface bears a heavier ornamentation of larger tubules arranged in about thirty posteriorly radiating rows. The canal is 10 mm. in length, the postero-inferior portion projecting cup-like downwards. (On the right side, at the origin of the lateral line, is a large hastate scale obviously representing a fusion of two units of the type of the first and the second lateral line scales of the left side.)

Posteriorly the lateral line scales gradually change in shape. The ninth scale (62) is roughly circular with triangular exposed portion about one-third of the total surface (Plate XLI). The tube bifurcates posteriorly and the inferior cup-like projection is much reduced. The exposed surface is covered with tubercles, those anteriorly being fairly large in an irregular group. The distal tubercles are slightly smaller, and are arranged in about twenty-five caudally radiating irregular rows. On the ventral surface on the tubule and branches are numerous extremely minute foramina which may be points of innervation.

The scales of the lateral line increase in size posteriorly and attain maximum size at about the sixteenth, remaining approximately constant until about the fortieth. Thereafter they decrease rapidly in size. The eighteenth lateral line scale (63, Plate XXXVIII) is ovoid, the exposed portion being subrhombic. The scale is 41 mm. in total length and 35 mm. in maximum width. The exposed portion is 30 mm. in height and 15 mm. in width, and is about one-fourth of the total surface. The tubule is only 6 mm. in length, and more normally perforation-like. It bifurcates into two main branches bordering the exposed area, the inferior of which has several superior apertures. There appear to be also several intermediate shorter posterior branches. The exposed surface is densely covered with twenty-eight distal more or less regular posteriorly radiating series of tubules, the tubules becoming marginally smaller.

The thirty-fourth lateral line scale (64, Plate XXXVIII), which occurs below the centre of the second dorsal peduncle (text-fig. 20), is more or less rectangular, 43 mm. in length and 33 mm. maximum breadth. The exposed portion is triangular with rounded base, 16 mm. in height and base 27 mm., and comprises one-sixth of the total area. The tubule commences 25 mm. from the posterior end and bifurcates, the two main

branches bordering the exposed area. Each has a superior aperture just beyond the bifurcation. The superior branch opens on to the dorsal surface of the scale. The tubules on the exposed portion are rounded, largest in the central portion of the triangle, smaller posteriorly, where there are twenty radiating series, with smallest at the anterior apex. Tubules are absent from an area in the upper posterior angle.

The fifty-first lateral line scale (65, Plate XXXIV), which occurs five rows before the origin of the principal dorsal caudal rays (text-fig. 20), is roughly a parallelogram, 35 mm. long and 22 mm. wide. The exposed portion is a triangle of base 15 mm. and height 15 mm., about one-sixth of the total surface. The main tubule bifurcates. The tubercles are rounded, large at the anterior apex and decreasing in size posteriorly, there being ten series marginally. The small area behind the terminal aperture of the superior branch of the tubule is naked.

The sixty-fourth lateral line scale (66, Plate XXXIV) occurs slightly nearer the origin of the supplementary caudal than the origin of the principal dorsal caudal rays (text-fig. 20). It is elliptical in shape, major axis 28 mm., minor 15 mm. The exposed surface is roughly about one-twelfth of the total area. It is triangular in shape and contains only twelve subequal sharp denticles. On the main tubule and on the two branches are several minute dorsal apertures.

The eighty-eighth lateral line scale (67, Plate XXXVII) is the twelfth lateral line scale on the supplementary caudal. It is pear-shaped, 11 mm. in length and 8 mm. maximum width. The width across the dorsal opening of the main tubule is 5 mm. The exposed portion is rhombic in shape. The main tubule is 6 mm. long, and very wide compared with the side branches. The denticles are very sharp, sub-equal, and comparatively long, there being eight on the exposed portion of the scale, which is almost half of the total area.

The remaining scales (61, 68-76, 80-88), of which figures are given in Plates XXXIII, XXXV, XXXVI, XXXVII, XXXIX, XL, and XLII, are representative of the areas from which they are taken (see text-fig. 20 in Folder-page II).

FLESH AND MUSCULATURE.

The taxidermist stated that the flesh of the *Coelacanth* was soft, almost plastic. The specimen had by then been dead for at least twenty-four hours. From this one may deduce that the fish might be expected to have only flabby muscles. The soft cartilaginous chordal sheath might be regarded as confirmatory. At the same time I have found a small section of the adductor muscle, and that is firm and strong.

It seems fairly certain that this fish is hardly likely to have had powerful

propulsive muscles capable of sustained effort. At the same time it would probably be capable of high output of energy for a brief period, after the manner of the Lophiid fishes. Thus among rocks, where it could stalk and pounce upon its prey, it would be a formidable creature. Mr. J. Omer-Cooper has suggested that it might use the second dorsal and the anal fins in swimming, or to assist it in crawling about. That appears reasonable.

OIL.

It was reported by the taxidermist that about one pint (about 600 c.c.) of oil had run from this fish, also that the flesh was oily, and that the chordal tube was partly filled with it. In fact, the taxidermist stated that oil "spurted" out where the first incision was made into the chordal sheath. Unfortunately the oil was thrown away, so little can be said about its nature.

The remaining parts of the fish are certainly abnormally oily, and the skin is impregnated with oil. The structure of the skin shown in Plate XLIV suggests that the lower cancellate portion is composed of oil-cells.

Even the bones remaining are saturated with oil, especially those on or bearing sensory canals. Preliminary extraction with chloroform was necessary before alizarin staining could be carried out. The conditions of many of the tabular bones indeed suggested that the sensory canal system had been bathed in oil.

The oil is probably of food-storage function. The high oil content of this fish is significant in relation to the theory of the "animal" origin of the "mineral" oil deposits of the world.

STRUCTURES OF UNCERTAIN IDENTITY.

Muscle Sheath (P) (Plates XXI and XXII; text-figs. 11 and 16).—This sheath was partly intact and had been stuffed by the taxidermist. I cannot give any positive information about its function. It probably contained some of the anterior optic musculature.

Palatine Canal (W) (text-fig. 7).—From the apex of the muscle sheath (P) there runs anteriorly a canal of moderate size. It lies on the skin of the roof of the mouth and runs almost straight forward beneath the wing of the parasphenoid, thus also beneath the ectethmoid (38) and the olfactory capsule, ending on the front margin of the upper jaw, above the dental plate of the prevomer. In view of its relation to muscle (P) it is a possible course for the following: buccal VII, palatine VII + palatine IX.

HABITAT.

It is by no means easy to explain how the existence of this species has not previously been suspected. No fossil remains from Africa are related to it more closely than those from other parts of the world.

The problem is essentially that of habitat. Judging from its general structure, this fish has survived almost unchanged from at least the Triassic. During that period it has lived in such conditions as to have left no obvious fossil remains, *e.g.* it may be a member of the earliest marine branch which has always lived in the sea, and in those parts of the sea of which the bottom has suffered no permanent elevation above sea-level. Under those circumstances the possibility of the discovery of remains would be very remote.

The species can scarcely frequent ordinary muddy- or sandy-bottomed areas within the 200-fathom line on our coasts, since it would most likely have been previously captured by trawlers. It is possible, indeed very probable, that this has happened, one report received stating that six such fishes had been taken in one trawl off the Natal coast, but discarded as unknown vermin. It is, however, certain that Coelacanths are, if not unknown, at least very rare in the marine areas mentioned, since repeated captures would inevitably have been reported. It is also reasonably certain that this species does not frequent rocky areas within the 50-fathom line, or it must have been taken by lines. Again there is the possibility that this has occurred. Our line fishermen are notoriously superstitious, and much opposed to pulling into the boat any strange creature. Still, the evidence is against there having been many captures of this Coelacanth by the line-boats of South Africa, which rarely operate at depths exceeding 40 fathoms.

Opinions have been advanced that this species is a wanderer from the depths of the ocean. Dr. White, of the British Museum, in a popular article (*Illustrated London News*, 1939, vol. cxciv, No. 5212, Supplement, text) advanced the opinion that "Our living Coelacanth almost certainly was a wanderer from the deeper parts of the sea to which its kind have retreated in the face of fierce competition with the more active modern types of fishes." A number of facts are in conflict with that opinion. This is no degenerate fish. It is obviously a predaceous carnivorous form, at least as agile and dangerous as some of the more sluggish fishes, such as the larger Serranids, which occur on our eastern shores. It is probably more of a "pouncer" than a speedy pursuer.

Against the bathybial habit may be ranged some degree of annulation in the circuli of the scales, the heavy squamation, and the eye of normal size. No bathybial form, not even those from only three hundred fathoms,

could possibly survive removal from the water by three to four hours, certainly not after having undergone compression and damage in the bag of the trawl net, and on the deck of the trawler under a few tons of other fishes. The weight of the evidence points to a habitat of moderate depth beyond the reach of line fishing, and with bottom conditions such that trawl nets cannot operate. This suggests rocky areas probably at depths of 80-150 fathoms, where the Coelacanth possibly crawl as much as swim, and stalk their prey.

It has earlier been indicated that there are grounds for suspecting that the Coelacanth may live on the rocky or ridged outer edge of the 40-60-fathom shelf which lies off parts of our eastern coast. It is not unlikely that as a result of the publicity attending the discovery of this specimen others will be brought ashore before very long. At the same time should my guess about the habitat have any foundation in fact, the capture of other specimens will remain a matter of chance, at least in so far as ordinary commercial fishing is concerned. On any rocky slope trawling is out of the question. In even still water line-fishing at depths of 100-200 fathoms would be of doubtful value, and uncertain. The strong current which runs in the area where the Coelacanthids are supposed to occur would render this next to impossible of operation. The Mozambique current flows there from the north-east at an average rate of 2.5-3 knots, often at a greater speed. Such a current renders bottom line-fishing at even 40 fathoms very difficult. The technical difficulties at 100 fathoms would be very great.

Since some archaic survivals among fishes are located in fresh waters, at least the possibility of that habitat for the Coelacanth should be considered. Had this fish come from fresh water it must have come *via* one of the neighbouring tidal rivers. Those that may be considered are the Kei, the Buffalo, and the Chalumna rivers, less likely the Fish and the Keiskama rivers, since the latter are relatively distant and downstream of the Mozambique current. In the Kei and Buffalo rivers are fairly long stretches of water of low salinity within the effect of the tides. It is just possible that not very plentiful and wary large fishes might manage to live there in comparative obscurity. They might secure sufficient food by raiding the more abundant marine life of the estuaries. It is, however, extremely unlikely that any large fishes could live in those conditions and remain unknown to the natives at least.

The inland waters of the rivers of the eastern Cape can scarcely be considered a possible habitat. They consist chiefly of a series of disconnected pools, whose scanty fauna would not provide sufficient food for such large fishes as the Coelacanth. Also no such large fish could possibly lurk unknown there.

It would be unlikely for a freshwater form to enter the sea, to descend as deep as 40 fathoms and to remain alive with apparently unimpaired vitality (shown by its living for $3\frac{1}{2}$ hours after removal from the water).

It may be considered extremely unlikely that this *Coelacanth* was a wanderer from a freshwater habitat.

I wish to express my gratitude to Dr. Stensiö, Dr. Westoll, Dr. Moy-Thomas, and Dr. Nielsen for gifts of their valuable works. Especially to Dr. Westoll for kindly undertaking the laborious work of correcting the proofs of this paper. To Mr. Norman of the British Museum for kindly correcting the proofs of preliminary papers. To Miss Lyle and Mr. Omer-Cooper for having placed at my disposal all the resources of the Zoological Department of this College, and to Professor E. D. Mountain for preparing sections of a tooth, and for helpful suggestions about its structure. To Mr. J. Sebba, B.Sc., for preparing and photographing the sections of a scale and of the skin, also for assisting with a part of the other photography. Also to numerous friends for assistance in the great labour involved in numbering of structures in figures and in checking the manuscript.

I am indebted to the National Research Council of South Africa for generous financial assistance (Carnegie Fund).

RHODES UNIVERSITY COLLEGE,
GRAHAMSTOWN,
June 1939.

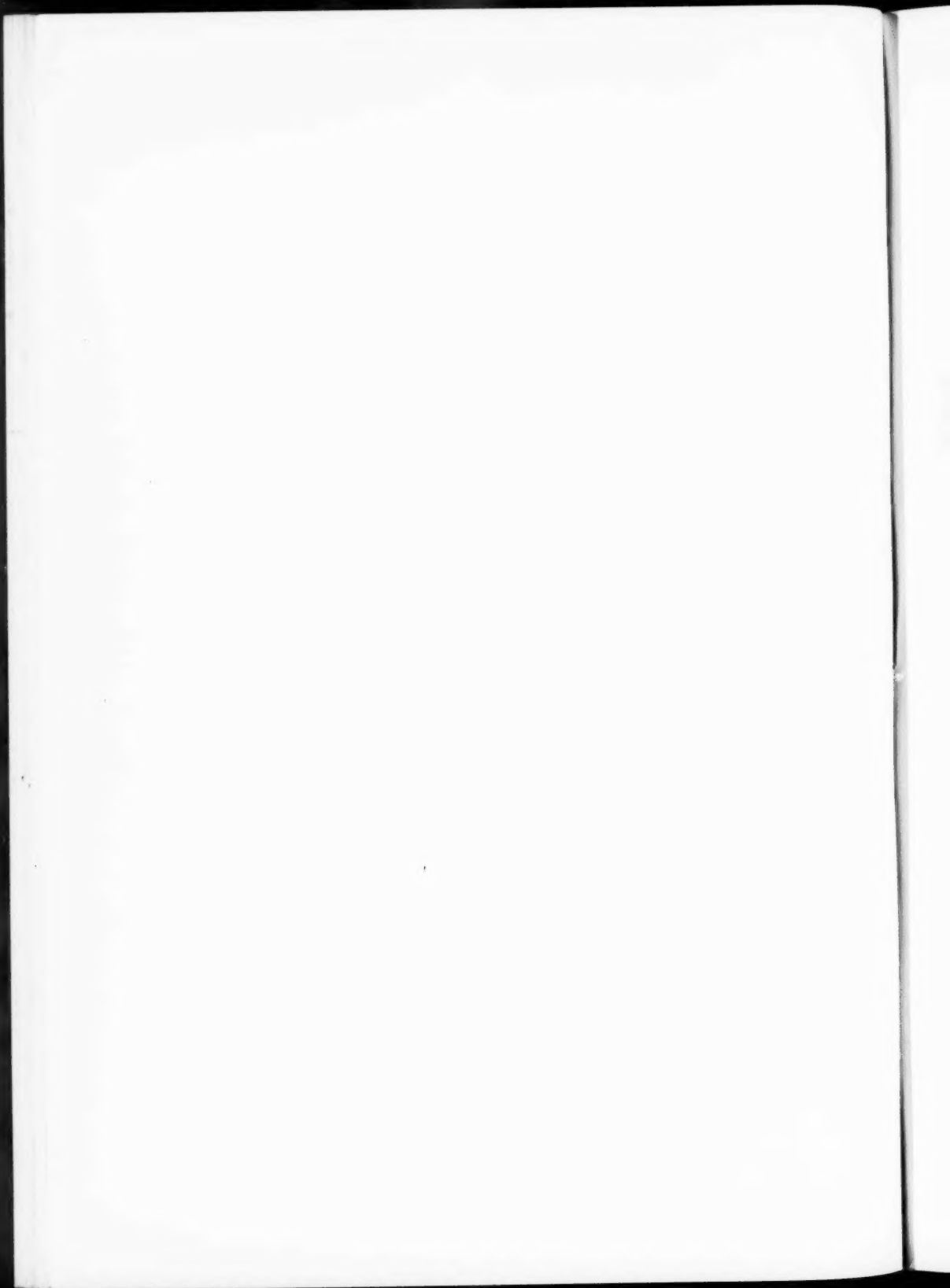
The Council desires to acknowledge the receipt of a grant from the National Research Council and Board towards the cost of publication of this paper.



Latimeria chalumnae Smith. 80125.
The small arrow shows the position of the spiracle.



Lalamia chalumnae Smith.
First dorsal fin with membranes restored, from right side.

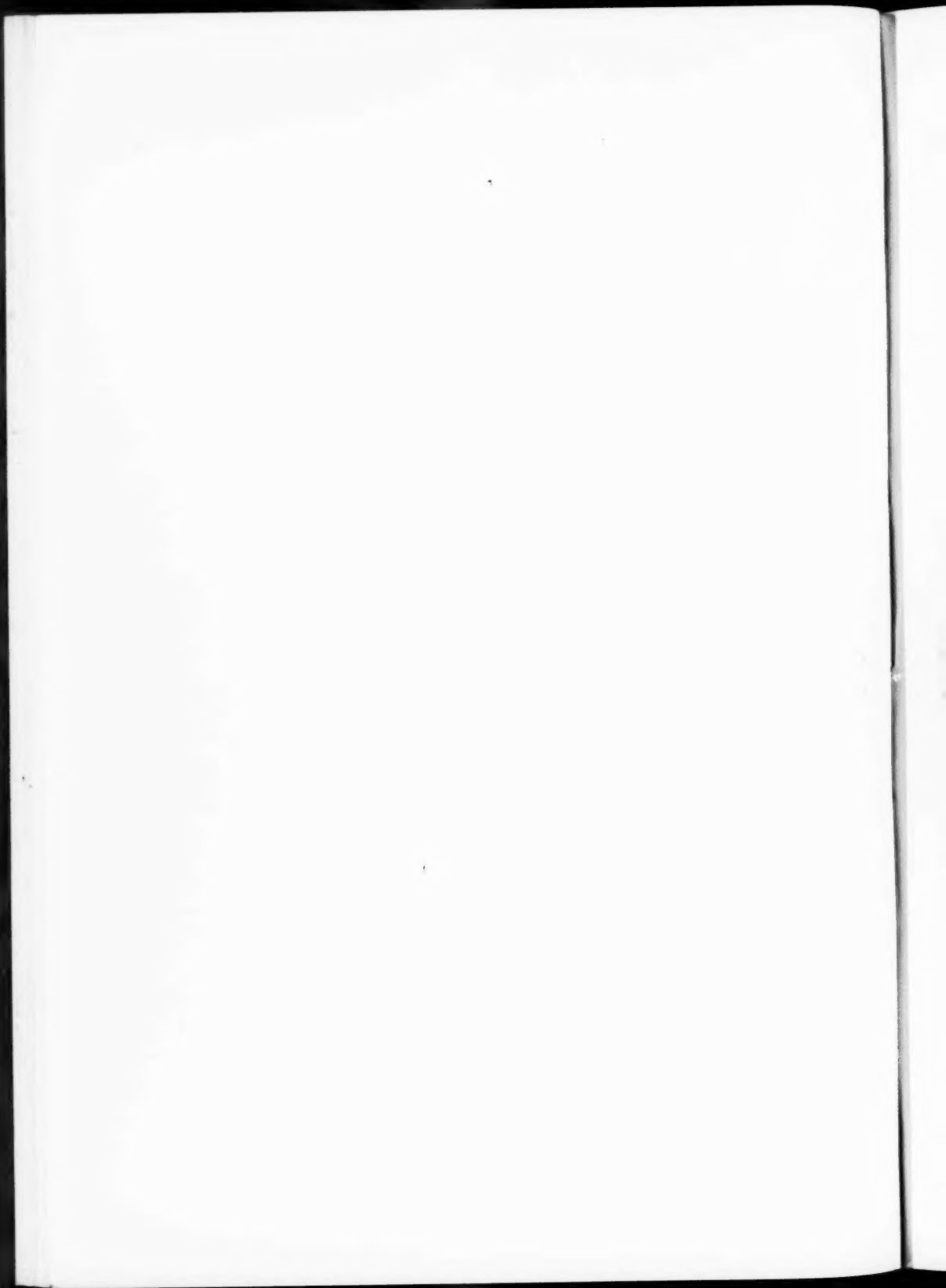




Lethinops chalumnae Smith.
Second dorsal fin. $\times 0.5$, showing some of the scaling. The small arrow shows the lateral line.

J. L. B. Smith.

↑
Nell & Co., Ltd.

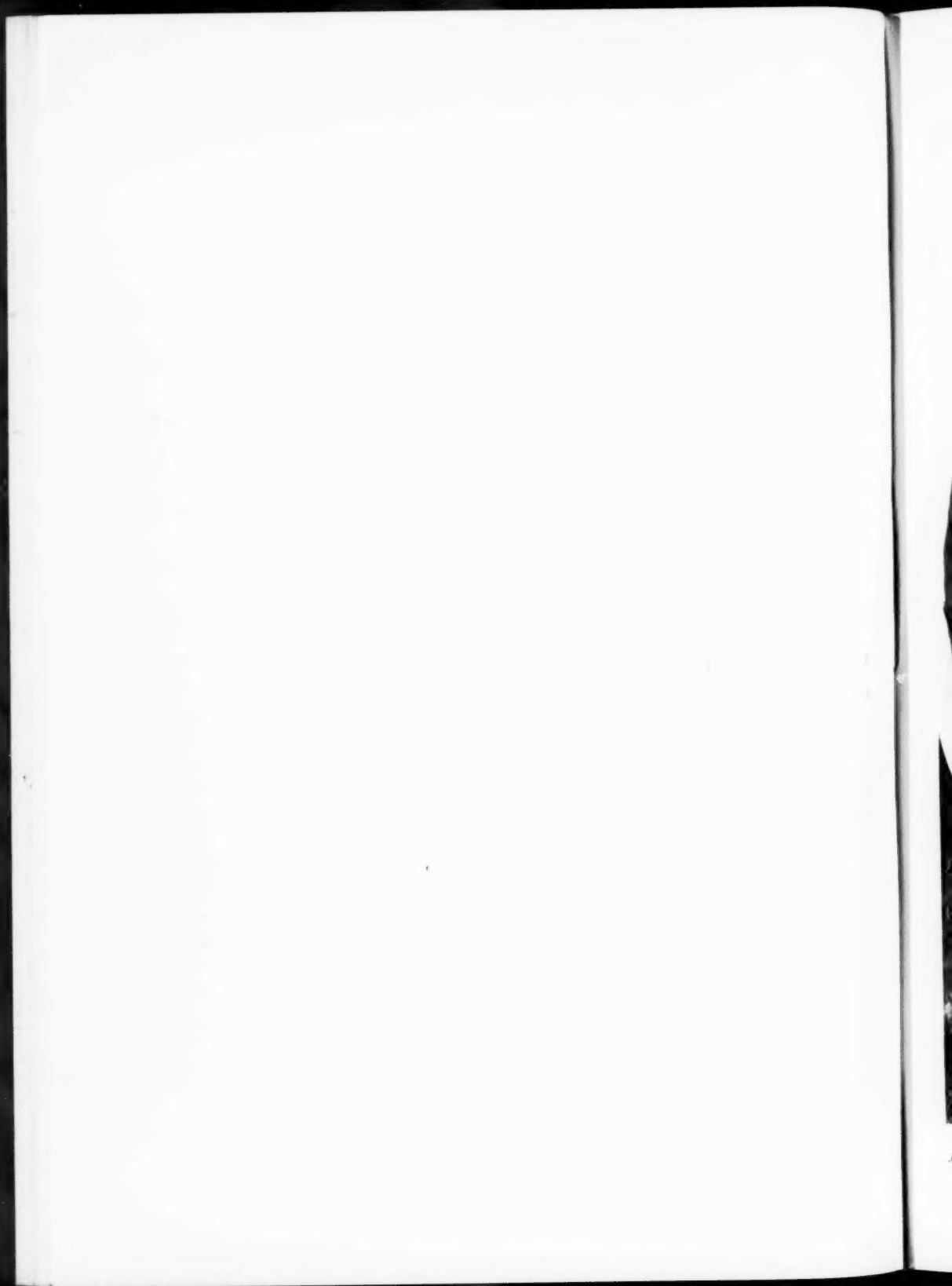




Latimeria chalumnae Smith. Caudal fin, left side. = 0.36.

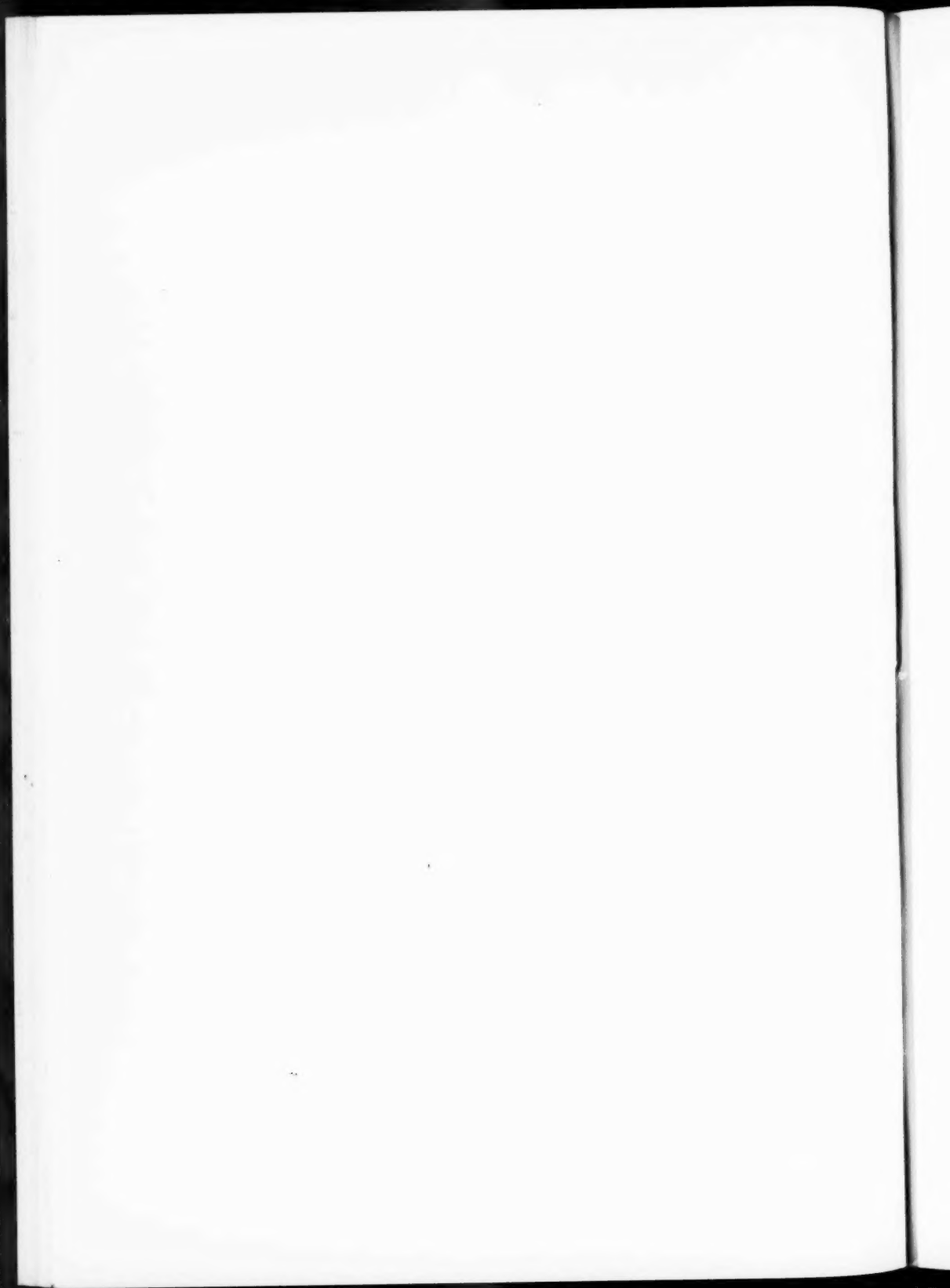
J. L. B. Smith.

Neill & Co., Ltd.





Letisiusia dolanensis. Smith.
Supplementary caudal fin, left side, 104.

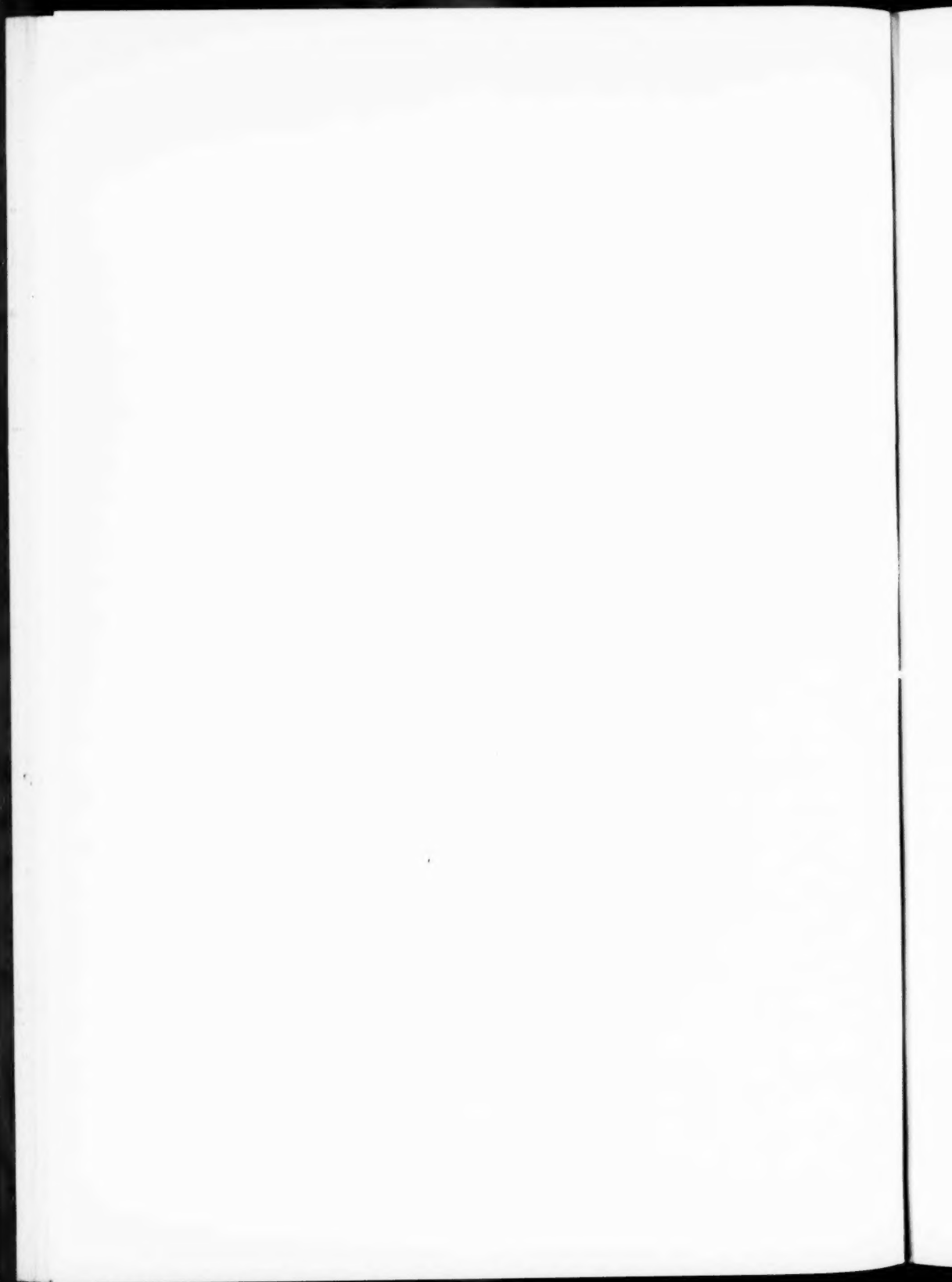




Latesia chalcidius Smith. Anterior principal ventral caudal rays, 1-4, showing some of the caudal scaling.
The small arrow shows the first short ray.

J. L. B. Smith.

Neill & Co., Ltd.

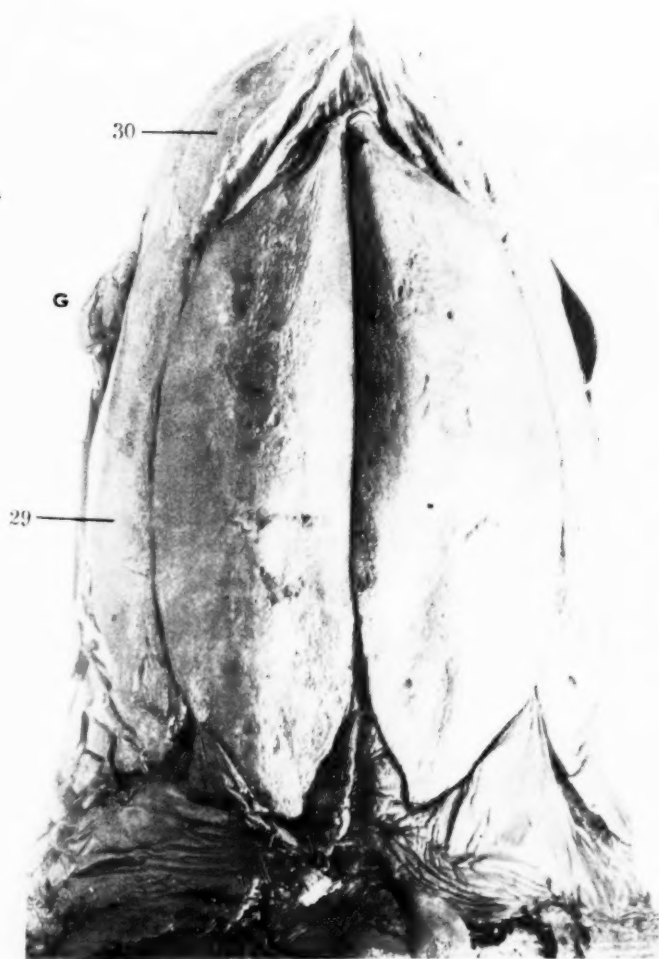




Latimeria chalumnae Smith.
Right pectoral fin. $\times 0.35$.



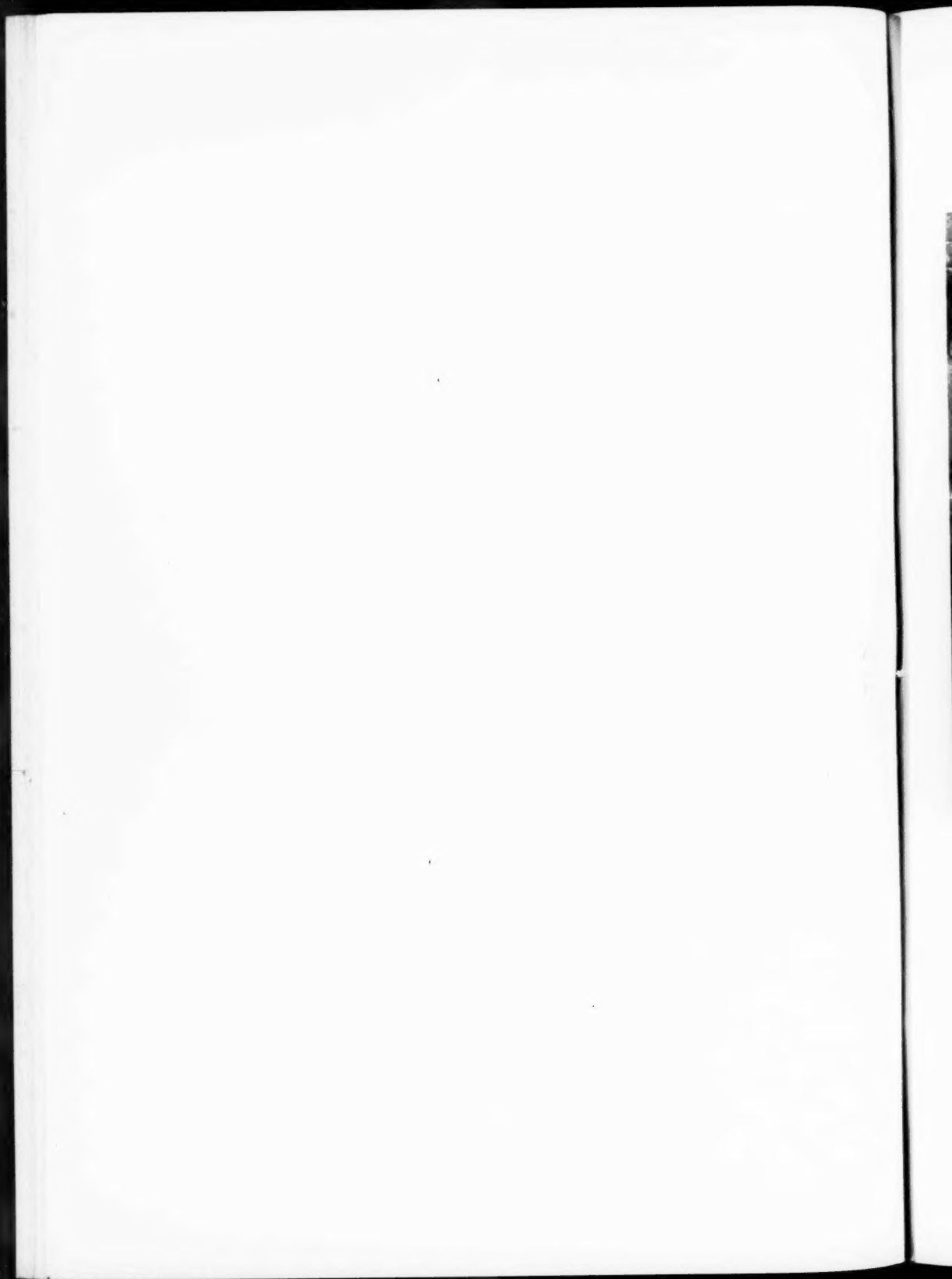
Latimeria chalumnae Smith.
Left pelvic fin. $\times 0.6$.



Latimeria chalumnae Smith.
Ventral view of head showing gular plates. $\times 0.45$. For explanation see
Folder-page I at end.

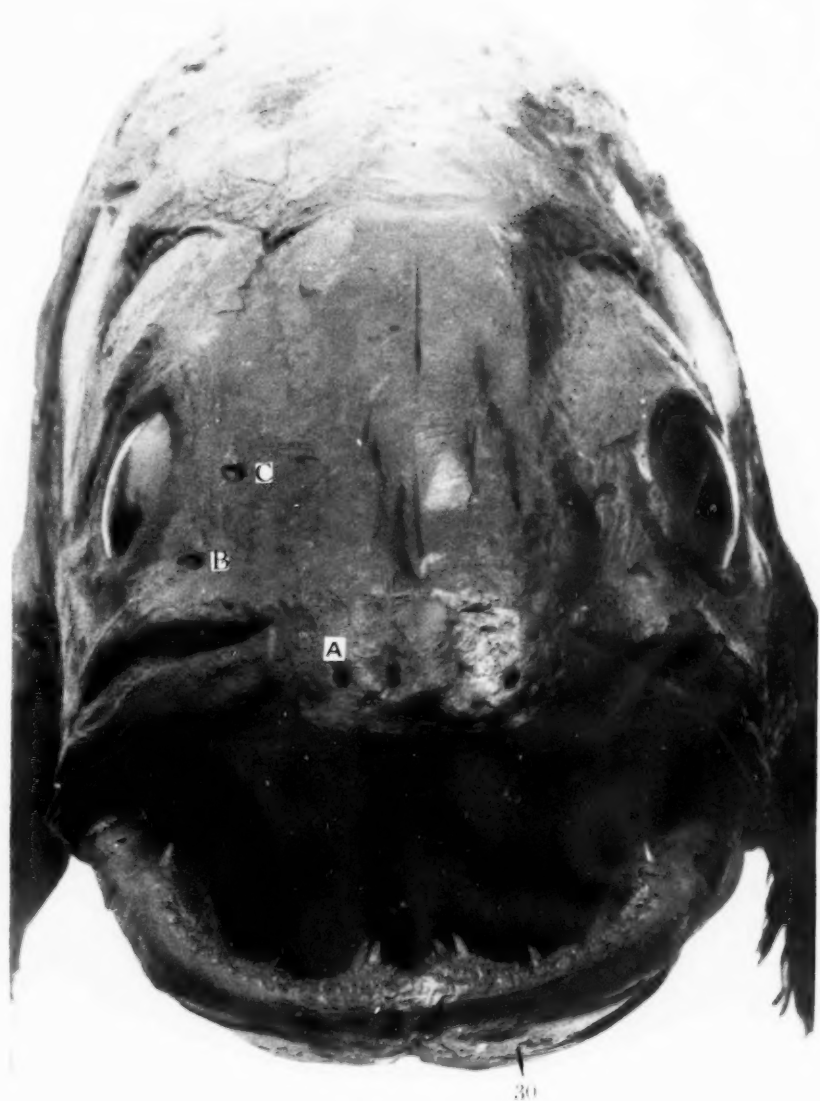


Latimeria chalumnae Smith.
Dorsal view of head. $\times 0.55$.





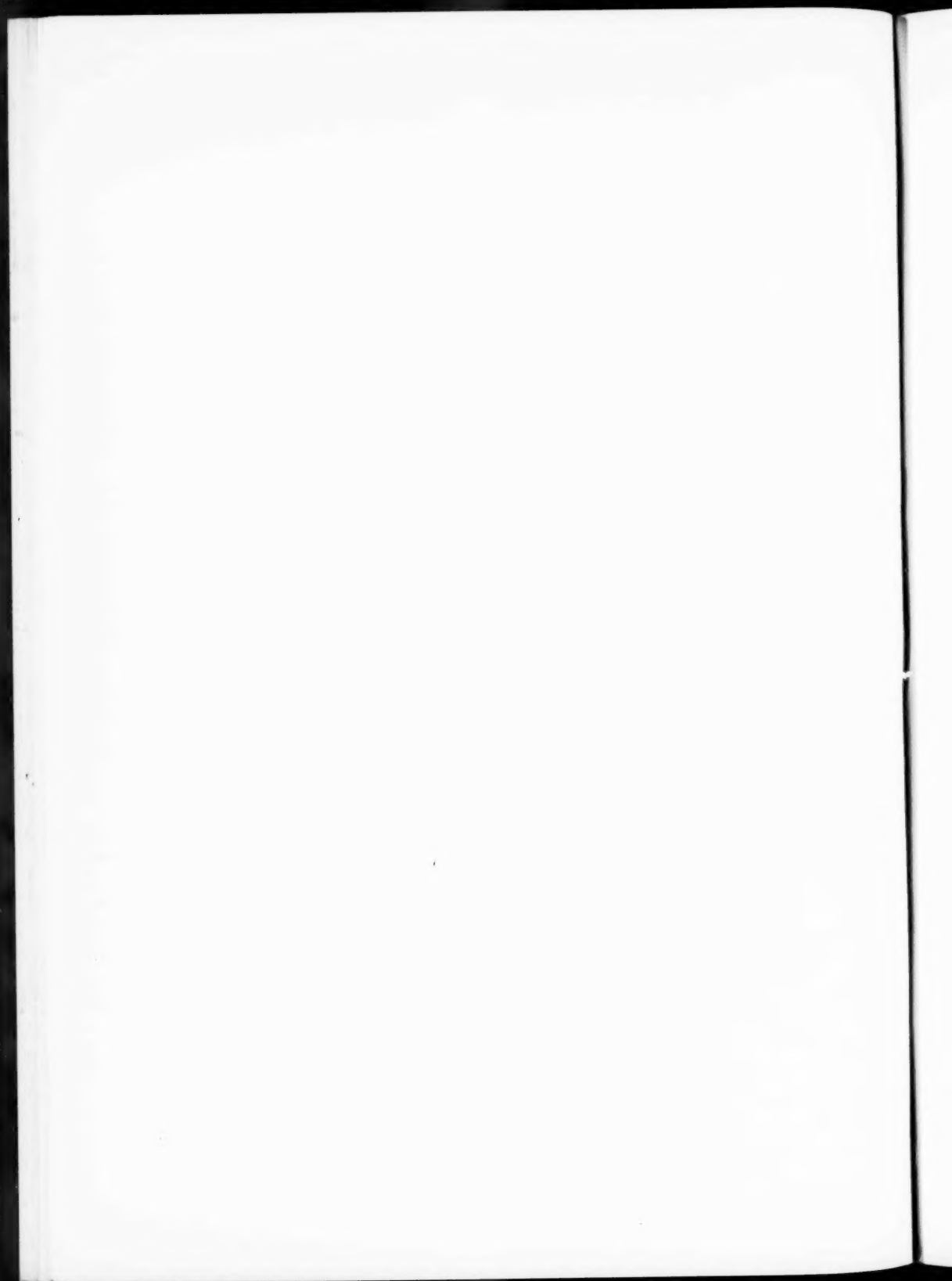
Latimeria chalumnae Smith.
Side view of snout. $\times 0.6$. For explanation see Folder-page I at end.



Front view of head. *Latimeria chalumnae* Smith.
×0.6. For explanation see Folder-page I at end.

J. L. B. Smith.

Neill & Co., Ltd.

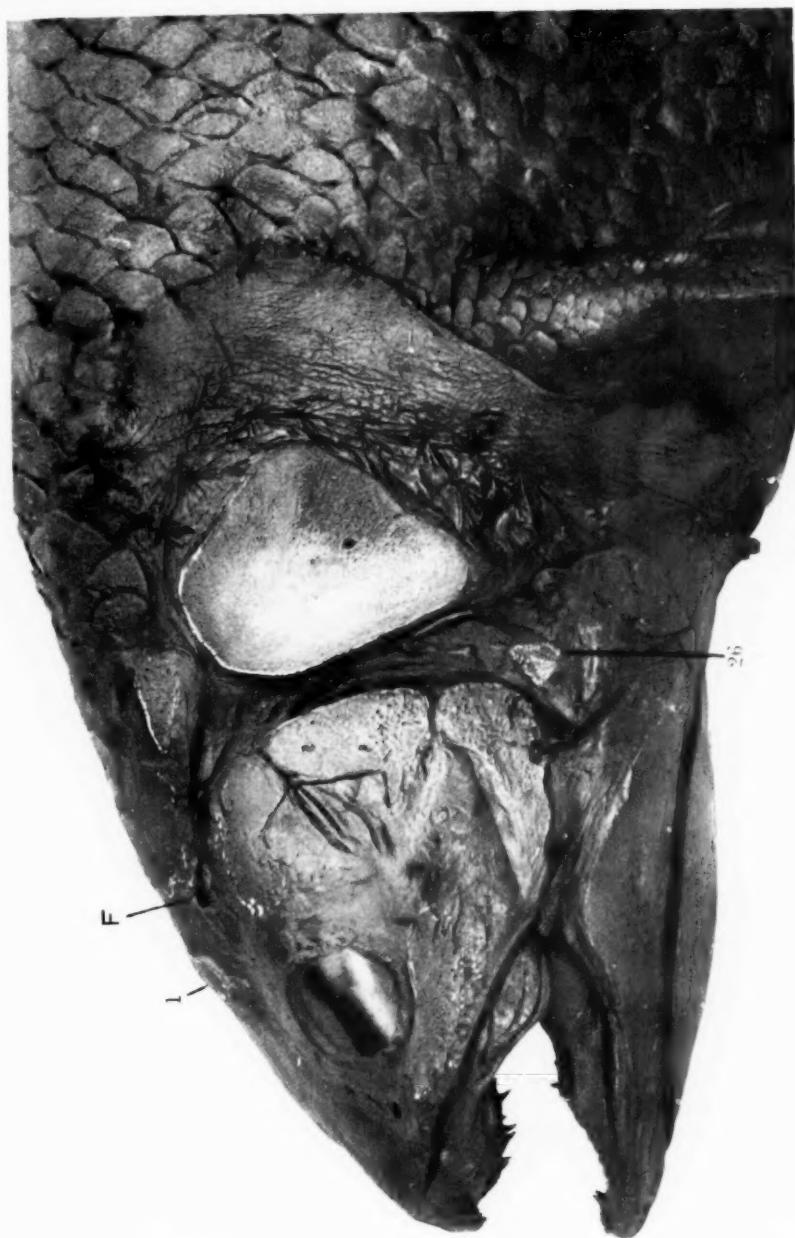




Ladimaria chalumnae Smith. Ventral view. $\times 0.125$.



Labyrinthodon chalumnae Smith. Head, right side. 1043. For explanation see Folder-page I at end.

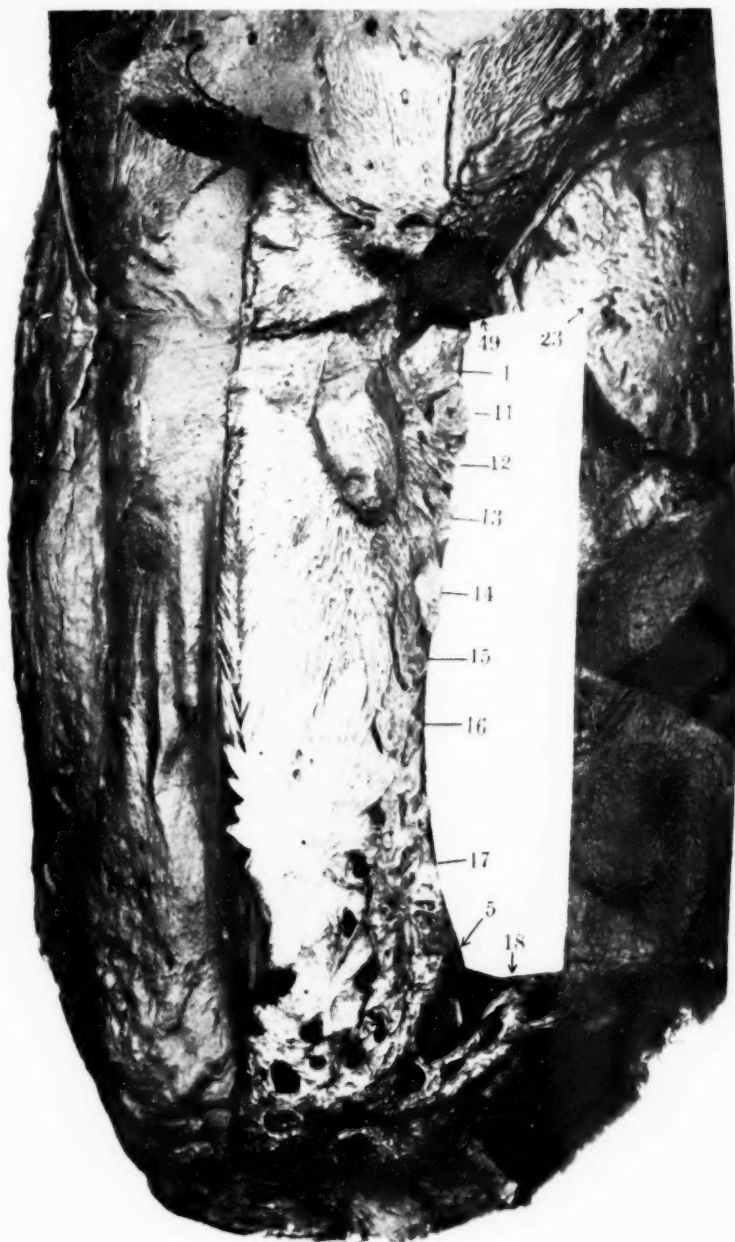


Latimeria chalumnae Smith.
Head, left side. — 0.39. (See text fig. 5.) For explanation see Folder page 1 at end.



Lethinaria chalumnae Smith.

Left: Reverse side of suborbital showing foramina. The bent wires are pushed into smaller foramina.
Top centre: Reverse side of postorbital. Remaining are cheek bones orientated, all -0.83. For explanation see Folder page 1 at end.



Latimeria chalumnae Smith.
Dorsal view of fronto-rostral area with skin removed on left side. 0-88.
(Compare text-fig. 3.) For explanation see Folder-page 1 at end.



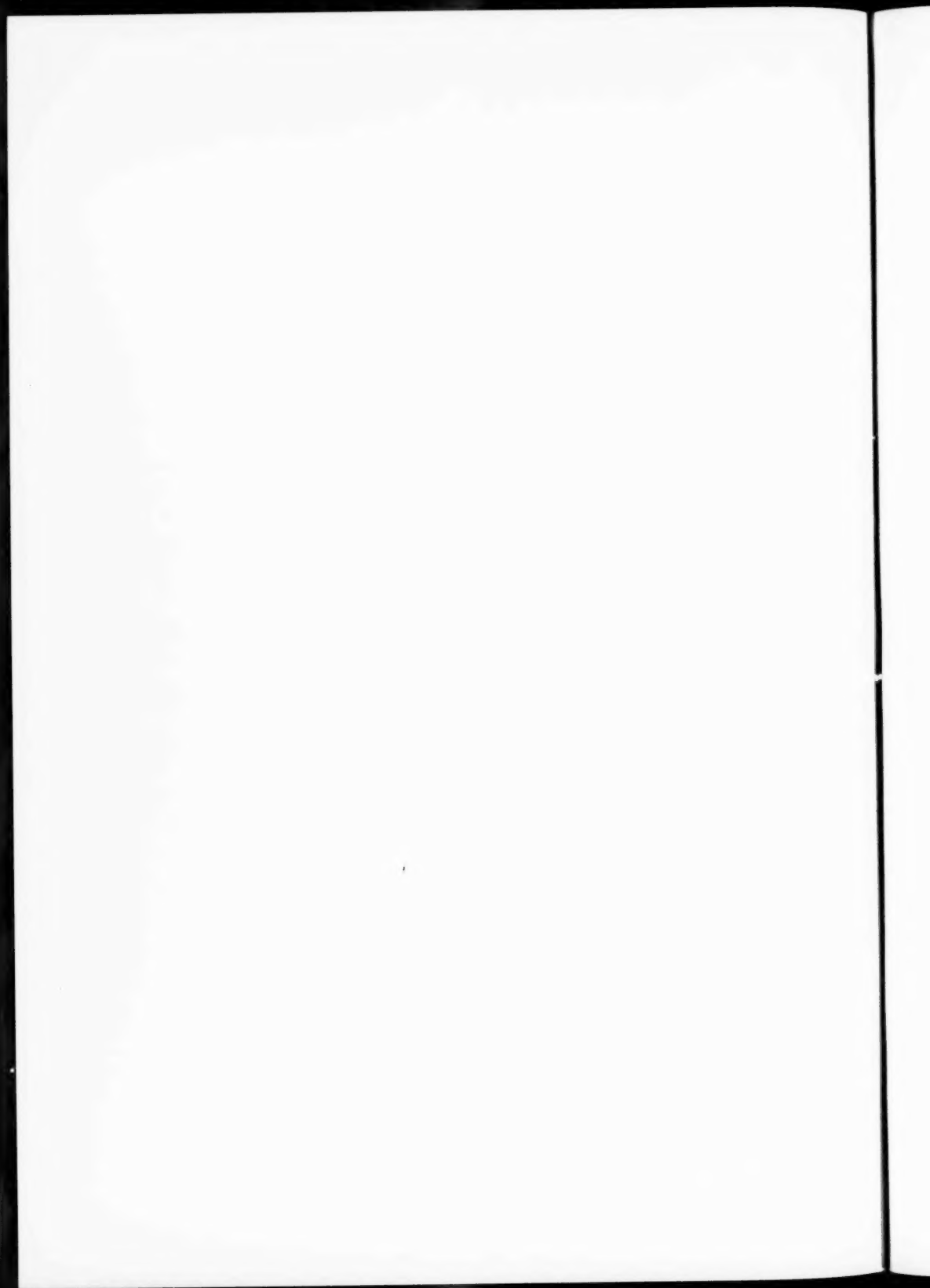
Latimeria chalumnae Smith. Fronto-rostrals. $\times 1-14$.

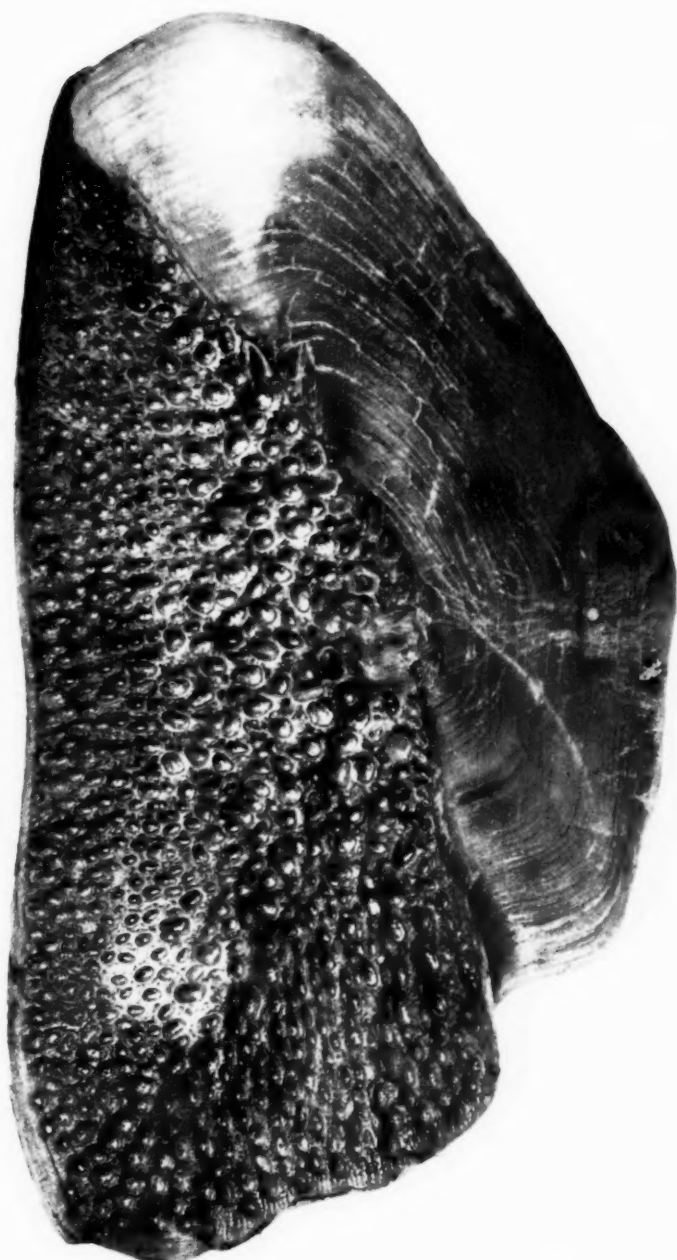
Left, above: Lower surface of frontal (1).

Left, below: Dorsal view of alisphenoid (1'). The cross shows position of sensory canal foramen.
For explanation see Folder-page I at end.



Latimeria chalumnae Smith. Rostro-nasals. $\times 1-9$.
For explanation see Folder-page I at end.

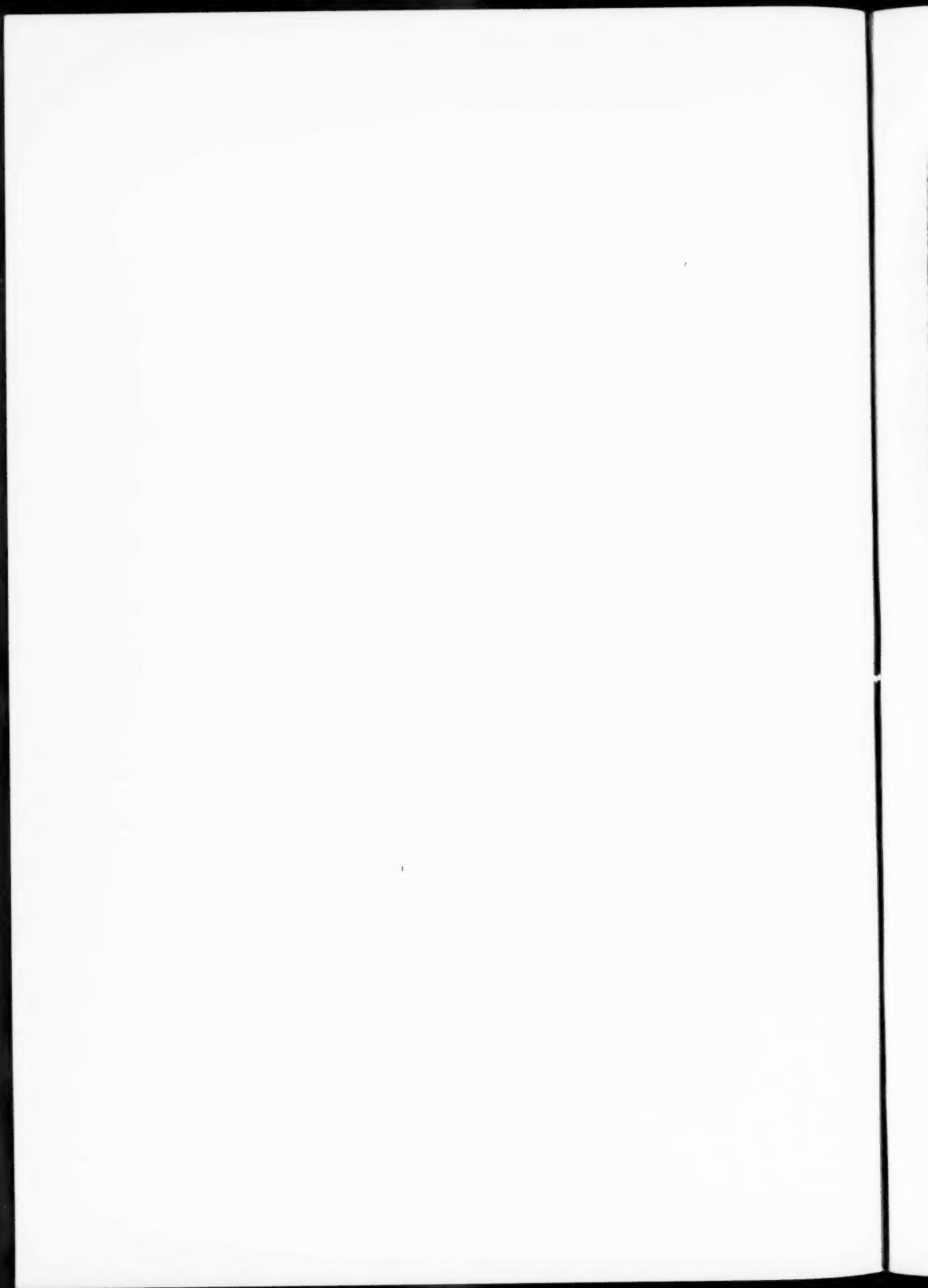




Lotimoria columnae Smith.
Right subopercular (27). $\times 3$.

J. L. B. Smith.

Neill & Co., Ltd.

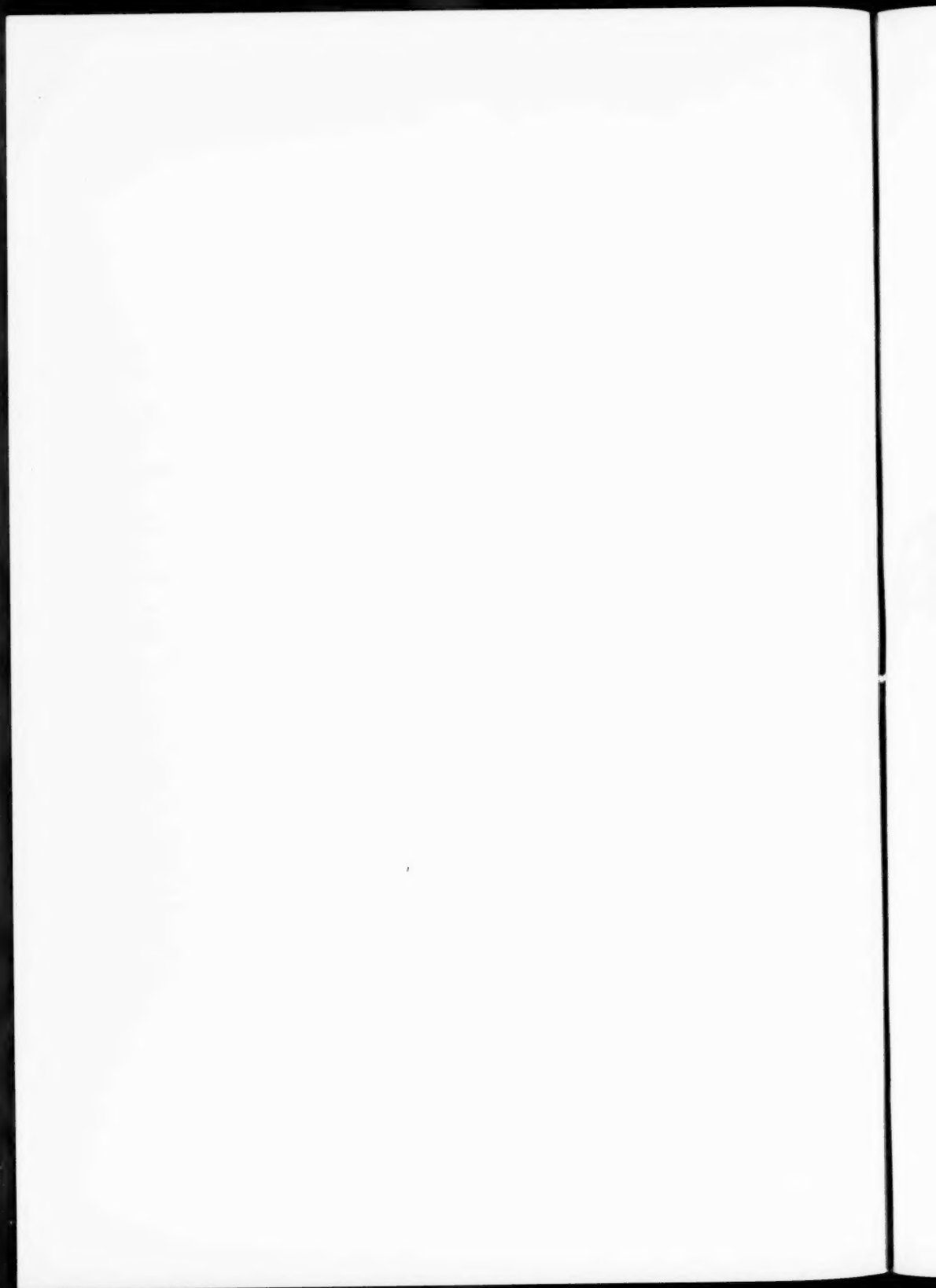




Leptonychia chalybeata Smith.
Left side of head with lateral dermal bones and parafacial series removed. (See text fig. 11.)
For explanation see Figs. 1 at end.

J. L. B. Smith.

Neill & Co., Ltd.



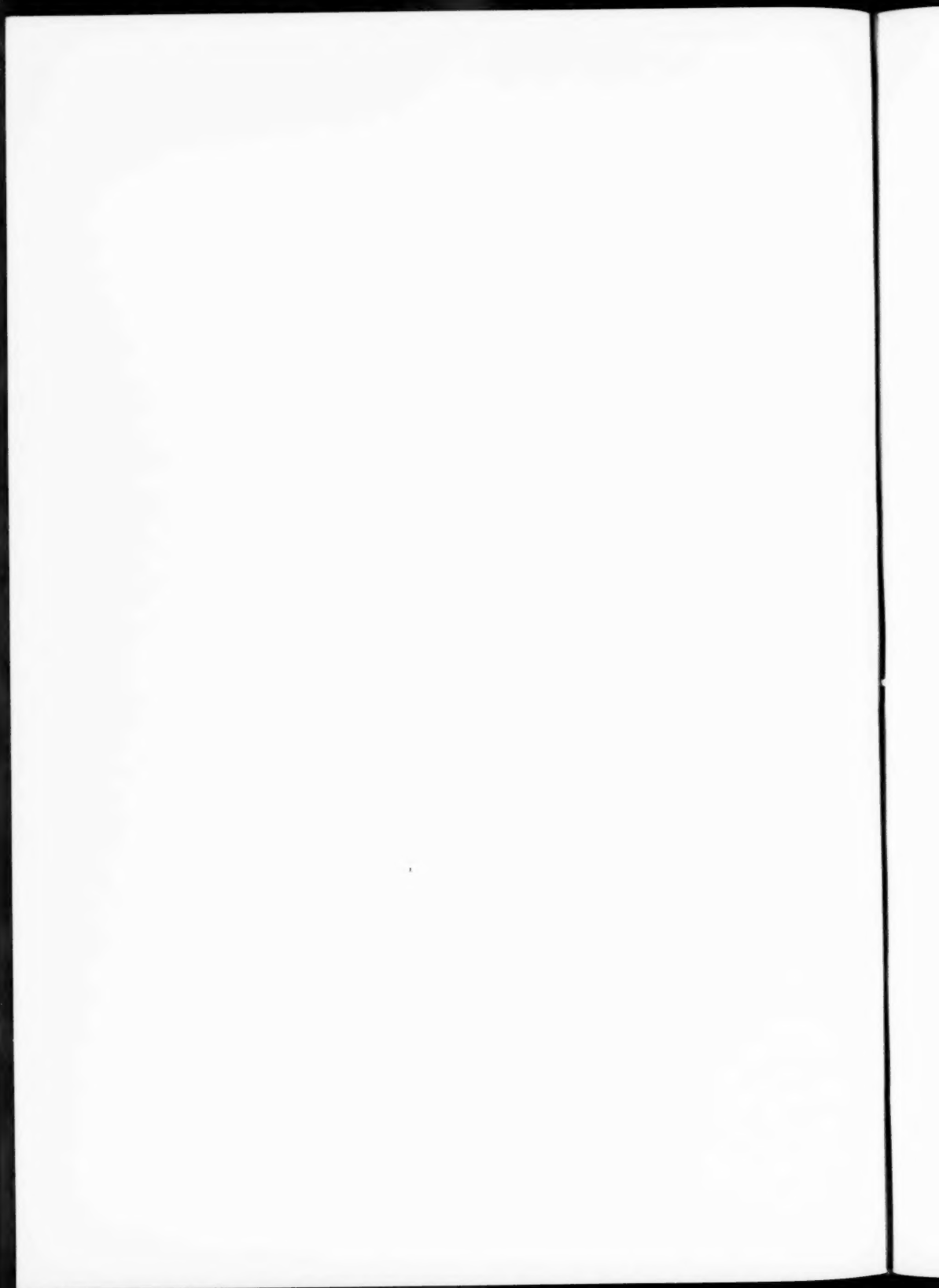


Latimeria chalumnae Smith.

Left side of head showing nasal cavities. $\times 1.43$. The two matches pass through the tubes from the lateral narial openings and show in the median sinus.
For explanation see Folder-page I at end.

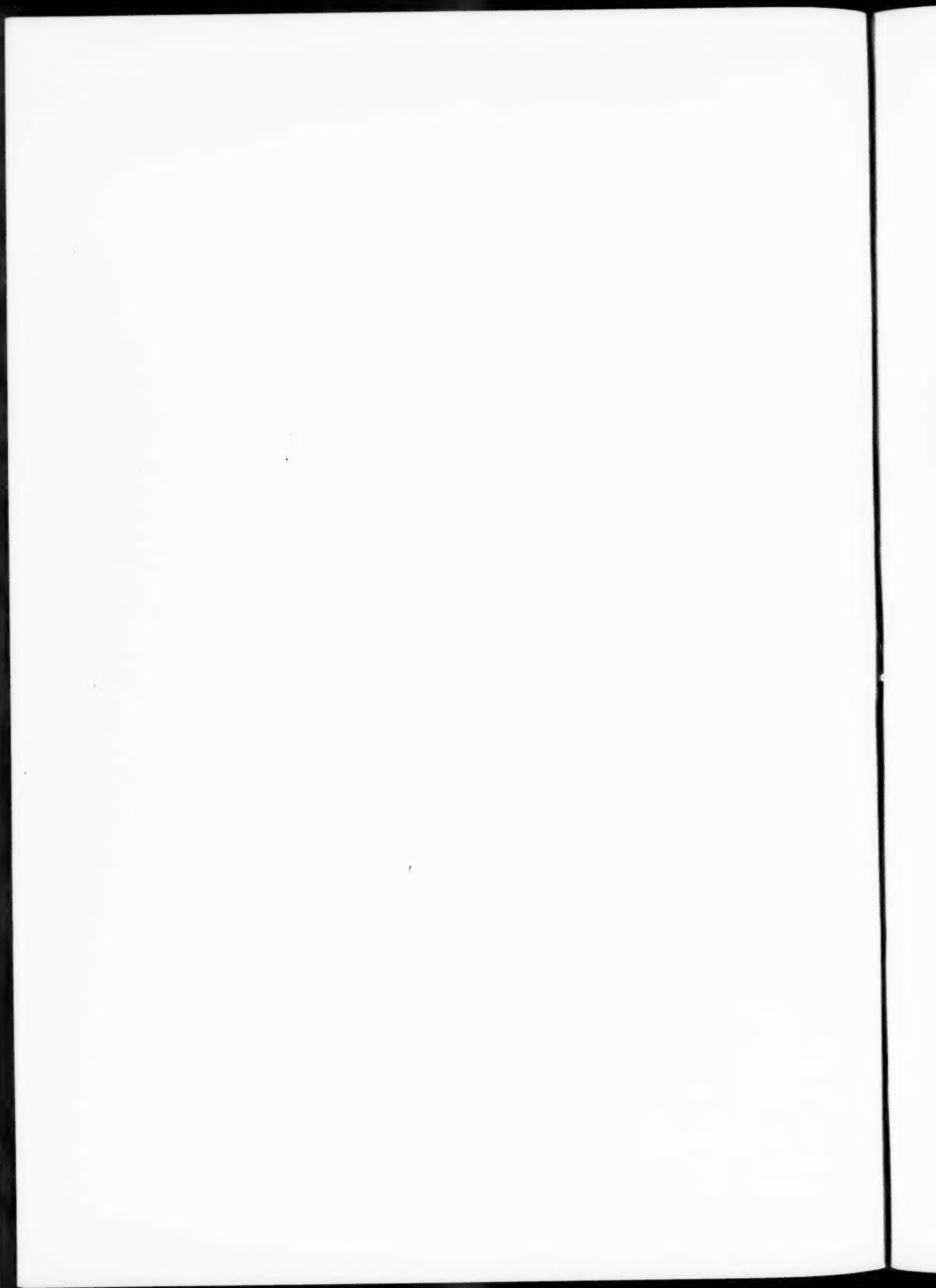
J. L. B. Smith.

Neill & Co., Ltd.



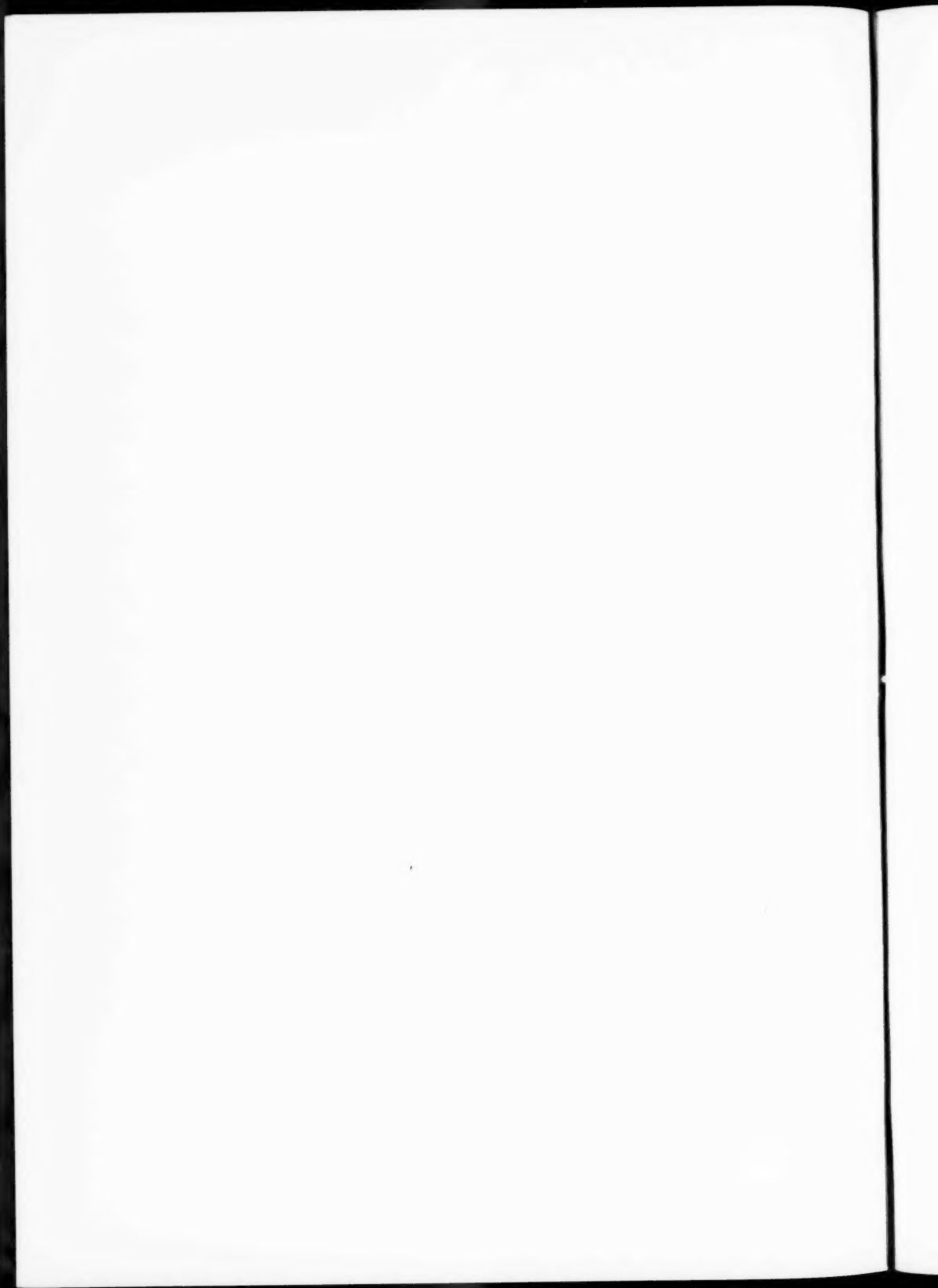


Latimeria chalumnae Smith.
Copula (45), dorsal. $\times 1.5$.



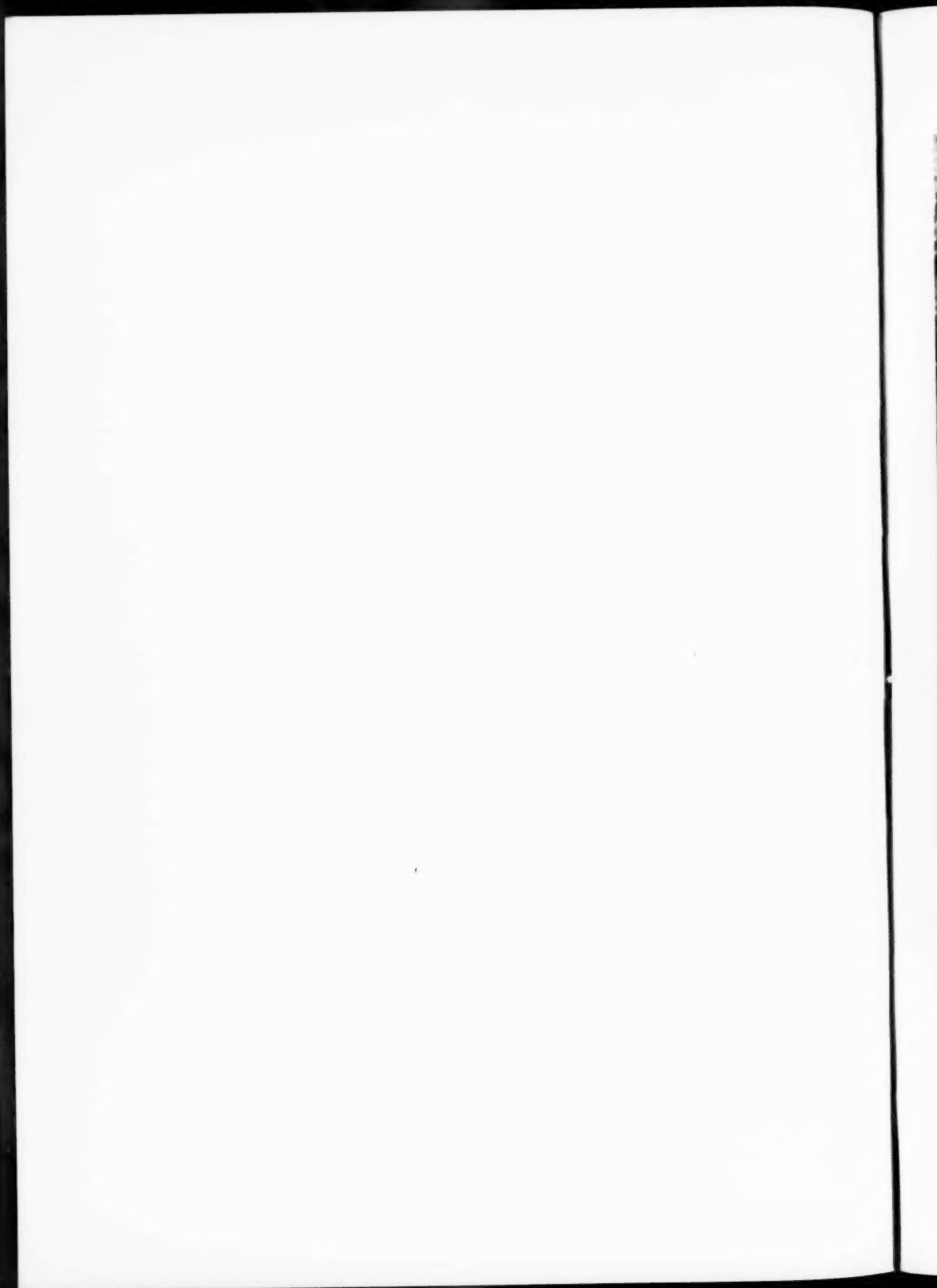


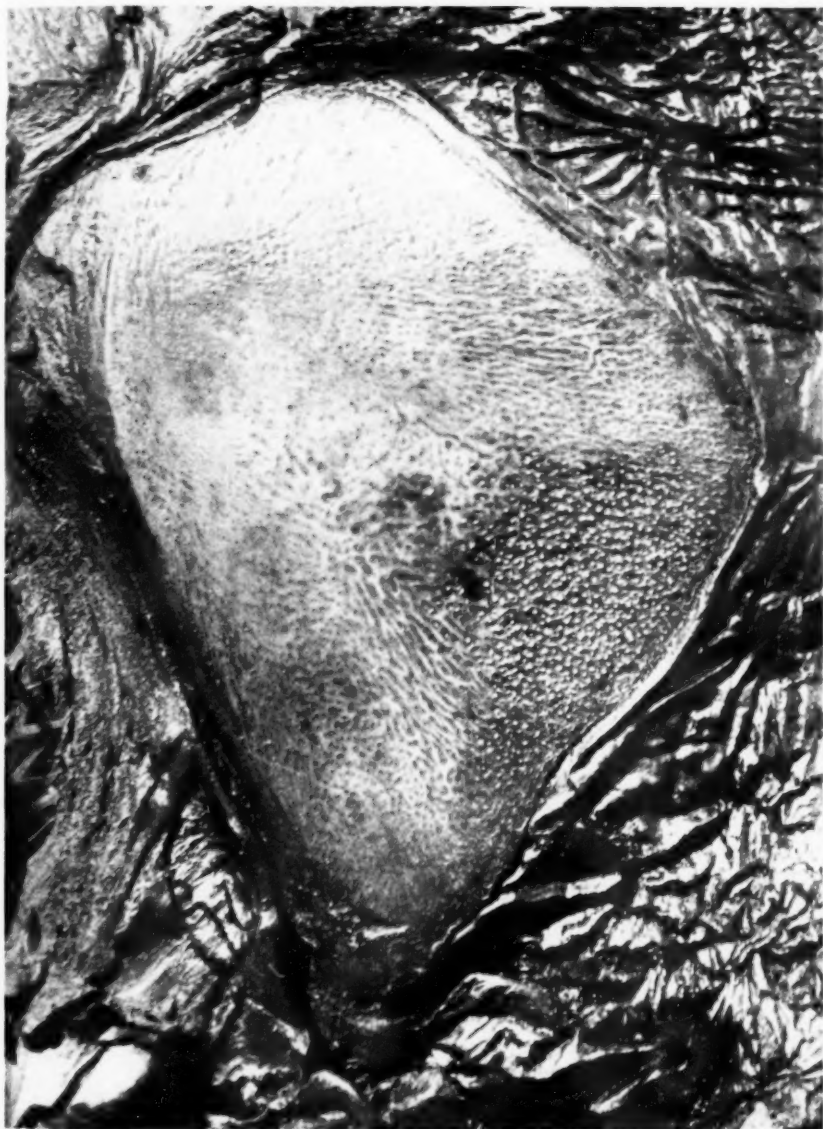
Latimeria chalumnae Smith.
Copula (45), ventral. $\times 1.45$.
For explanation see Folder-page I at end.





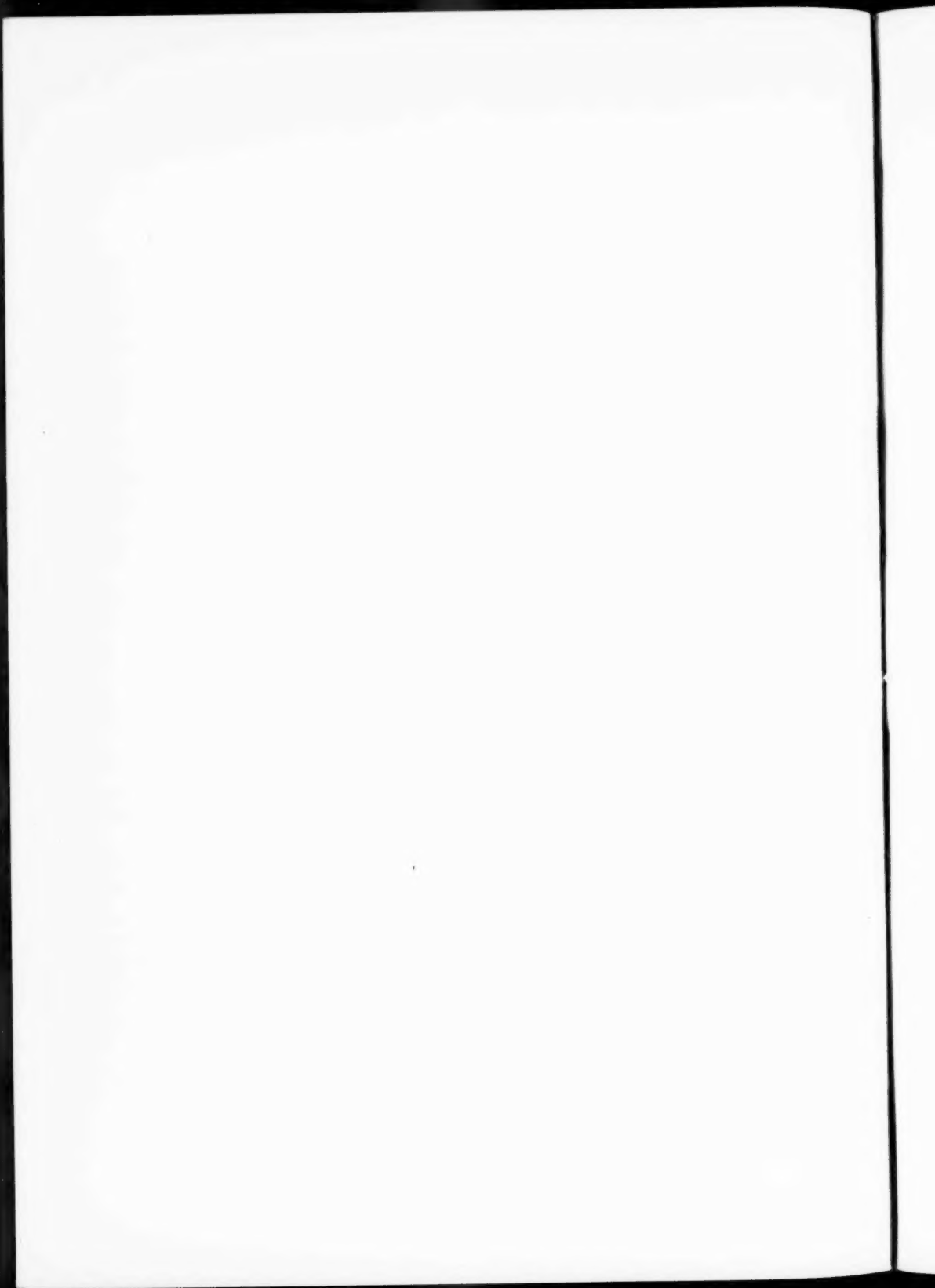
Lutimera chalumnae Smith.
Ramus of lower jaw, left side - 074. The arrow indicates the position and angle of entry of mandibular canal. The white blotch below the arrow-head marks the hind end of the hinder branch of the canal. For explanation see Folder-page 1 at end.

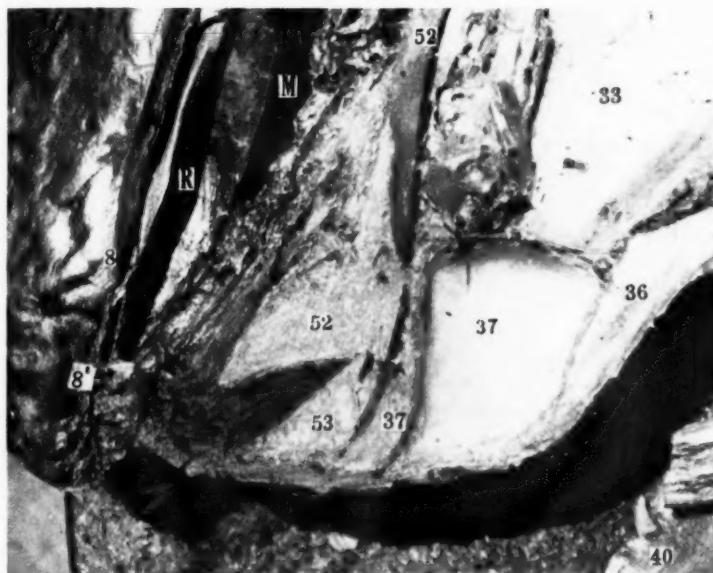




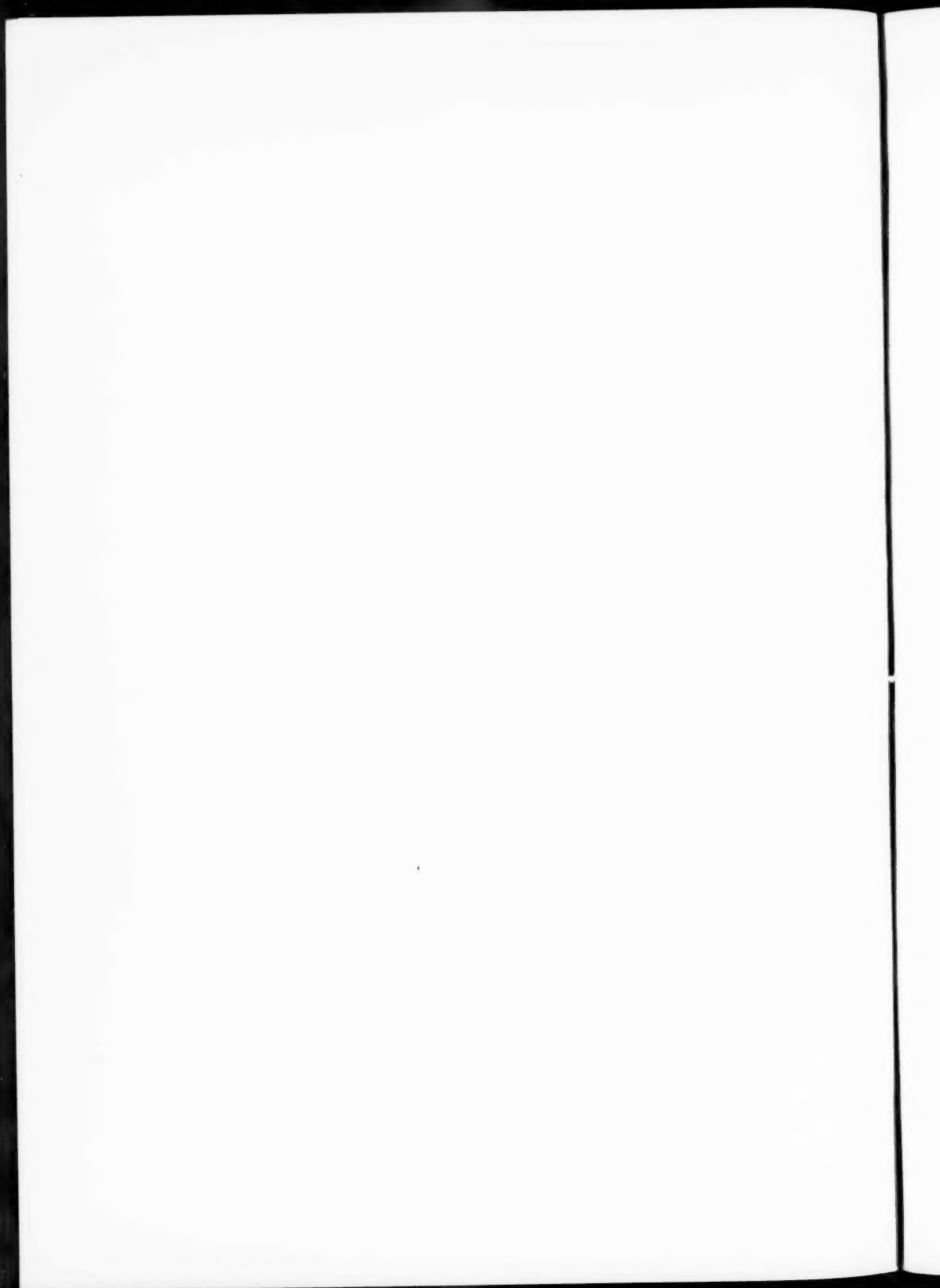
Latimeria chalumnae Smith.

Left opercular, $\times 1.1$. The hole among the tubercles is artificial.





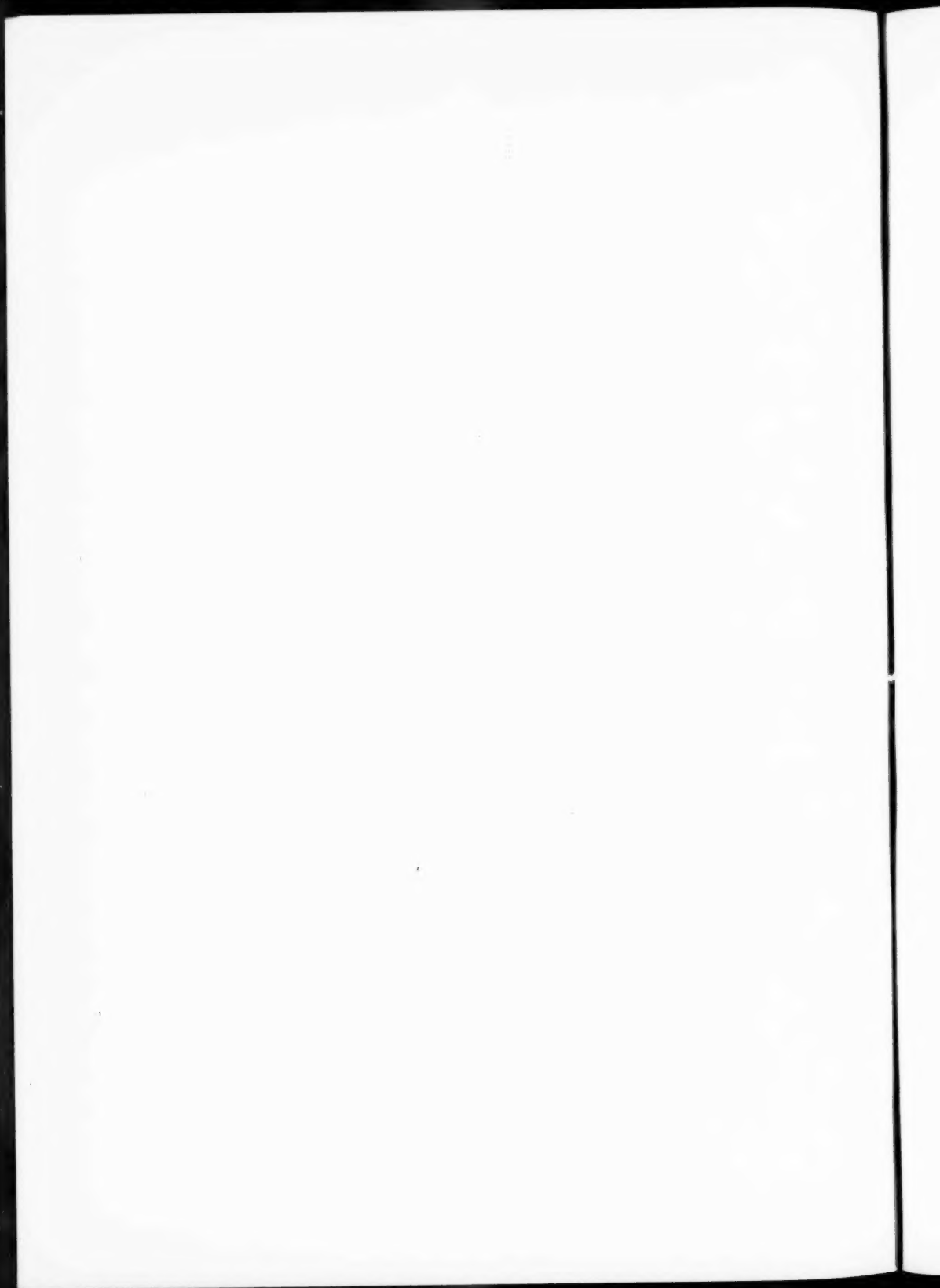
Latimeria chalumnae Smith.
Palatal roof ossifications from above, slightly left. Natural size.
For explanation see Folder-page I at end.





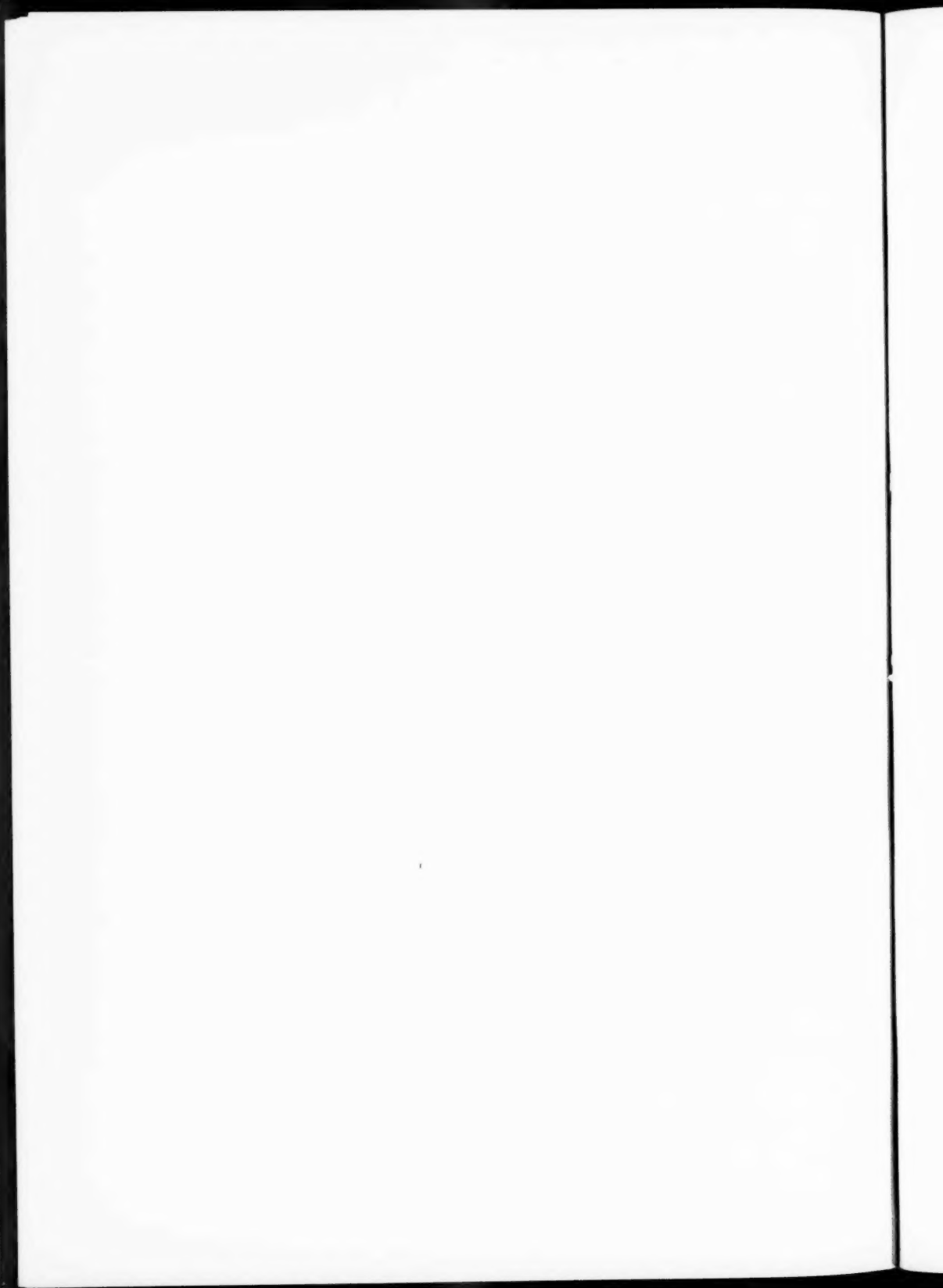
Latimeria chalumnae Smith.

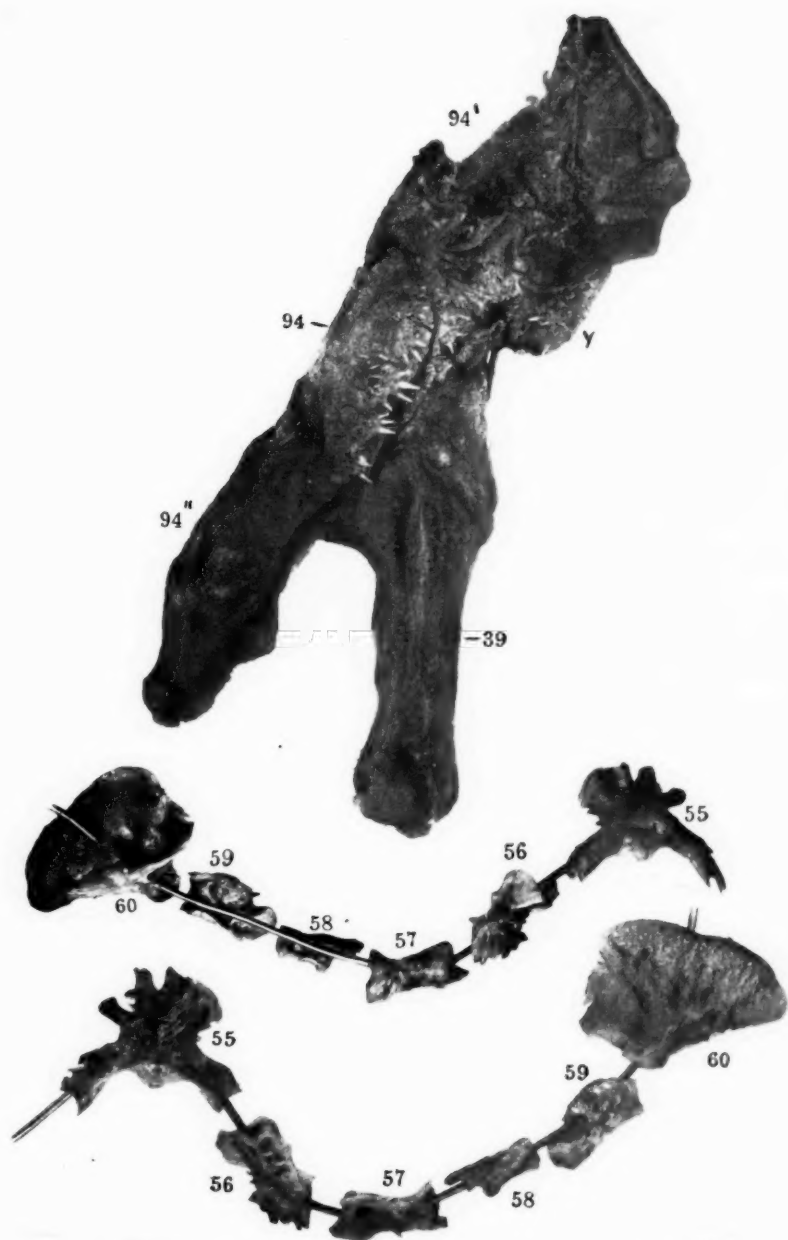
Temporal region. Upper, $\times 0.87$. Lower, $\times 0.7$. Inset on left, antotic ossicle (92), $\times 1.3$; upper: Exterior view, lower: View of base. For explanation see Folder-page I at end.





Lolioria chalumnae Smith.
19th lepidotrich of ventral principal caudal. *On left*: two lateral segments, $\times 145$. The upper arrow marks where the ray emerges from the body. The lower marks the point to which articulations are clearly visible. *On right*: upper portion of segment, $\times 25$.

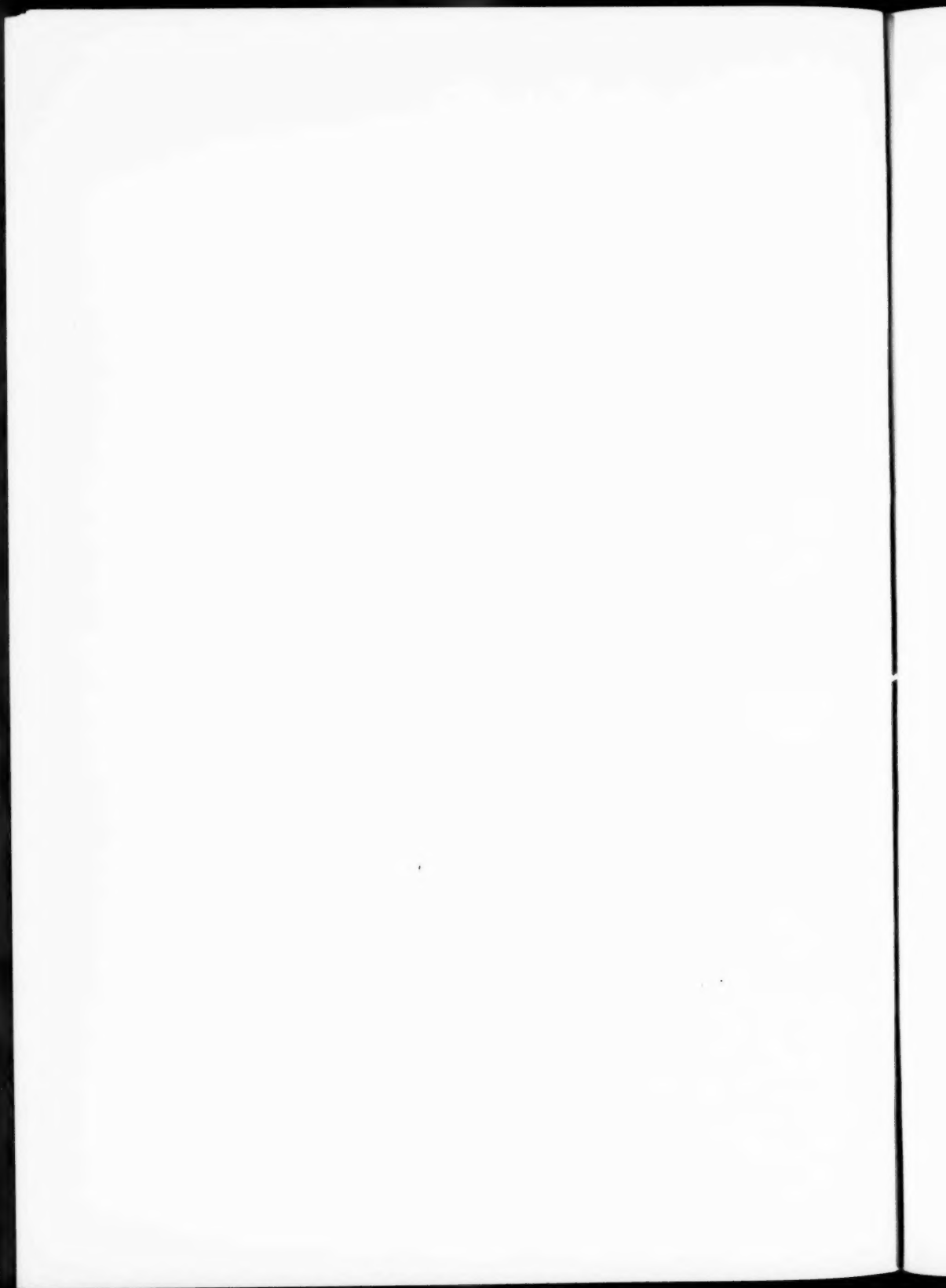


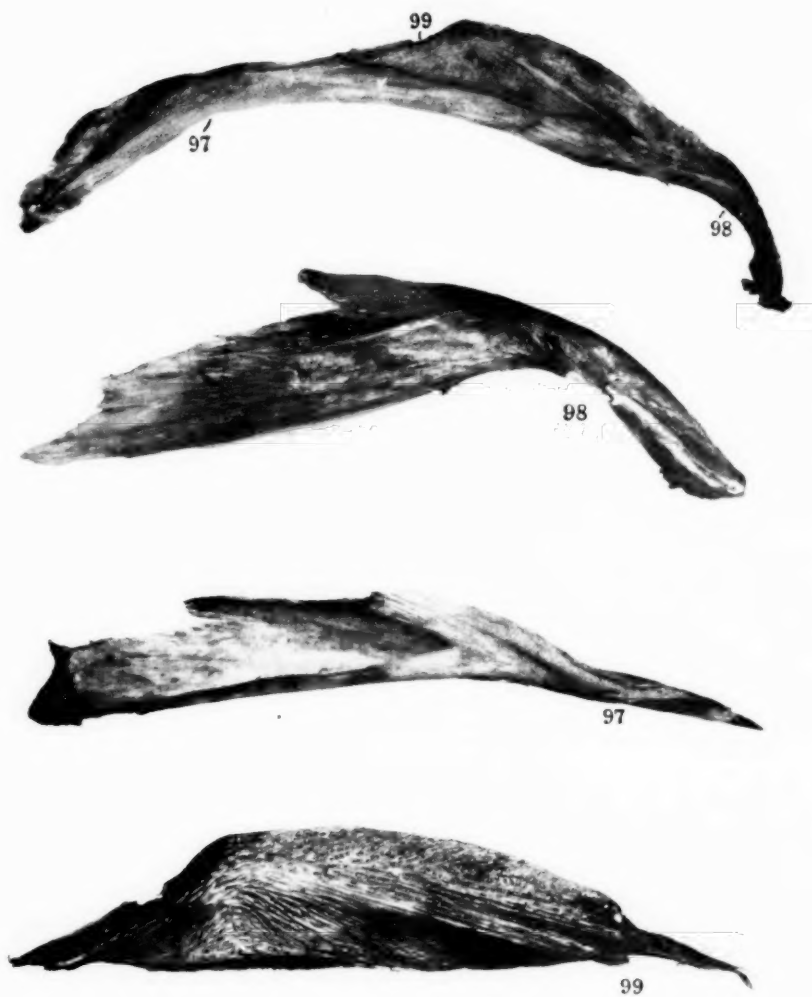


Latimeria chalumnae Smith.

39-94, Hyomandibular system from within, $\times 0.85$. (See text-fig. 13.) 55-60, Extrascapular chain.

Upper: Ventral view, $\times 1.0$. *Lower*: From above, $\times 1.15$. The connecting wire shows the course of the canal. For explanation see Folder-page I at end.

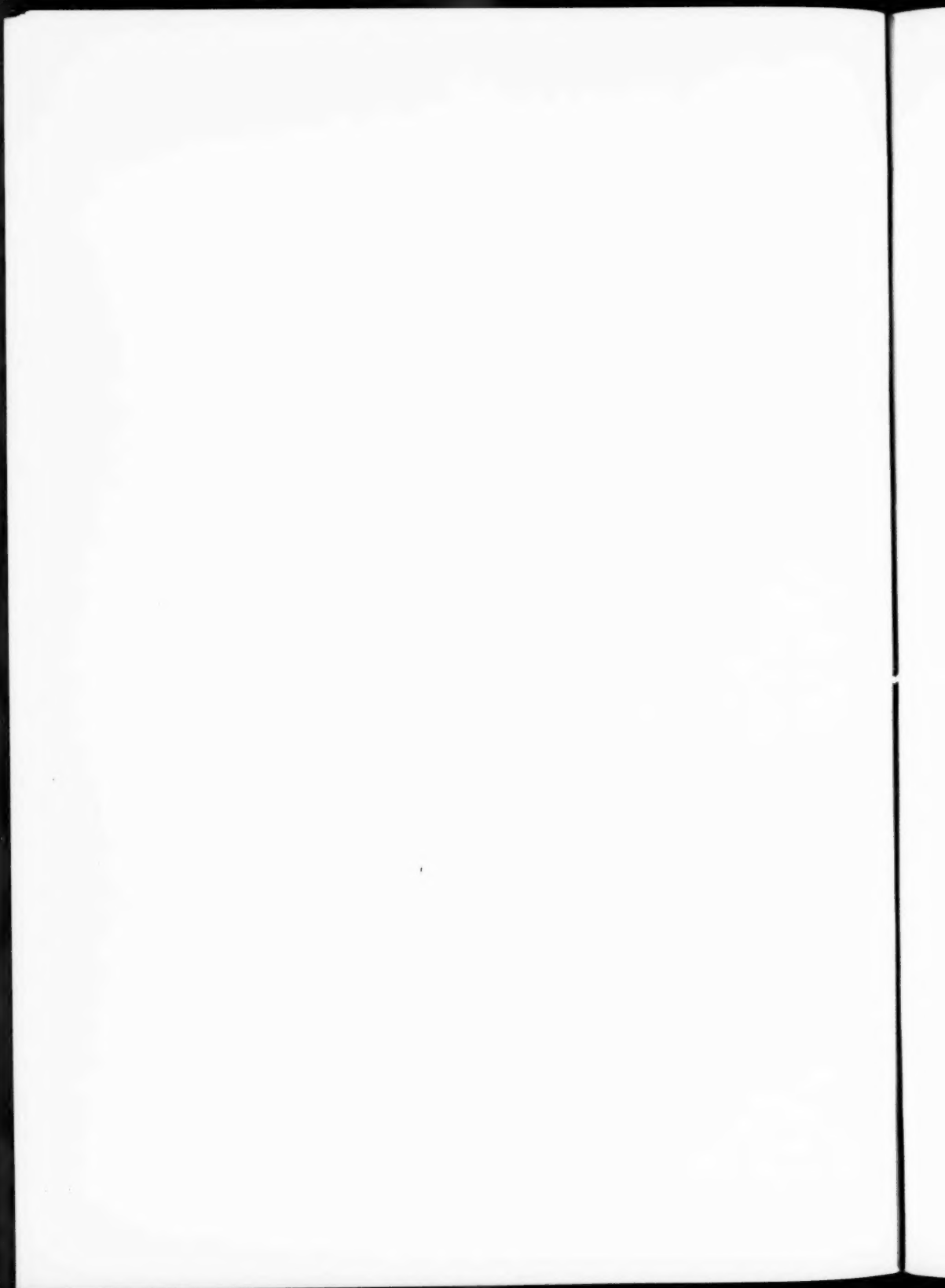




Latimeria chalumnae Smith.

Above : External view of shoulder girdle complex, $\times 0.45$.

98, Clavicle alone, $\times 0.9$. 97, Cleithrum alone, $\times 0.5$. Inner view. Extracleithrum alone, $\times 1.0$.
(See text-fig. 1.)

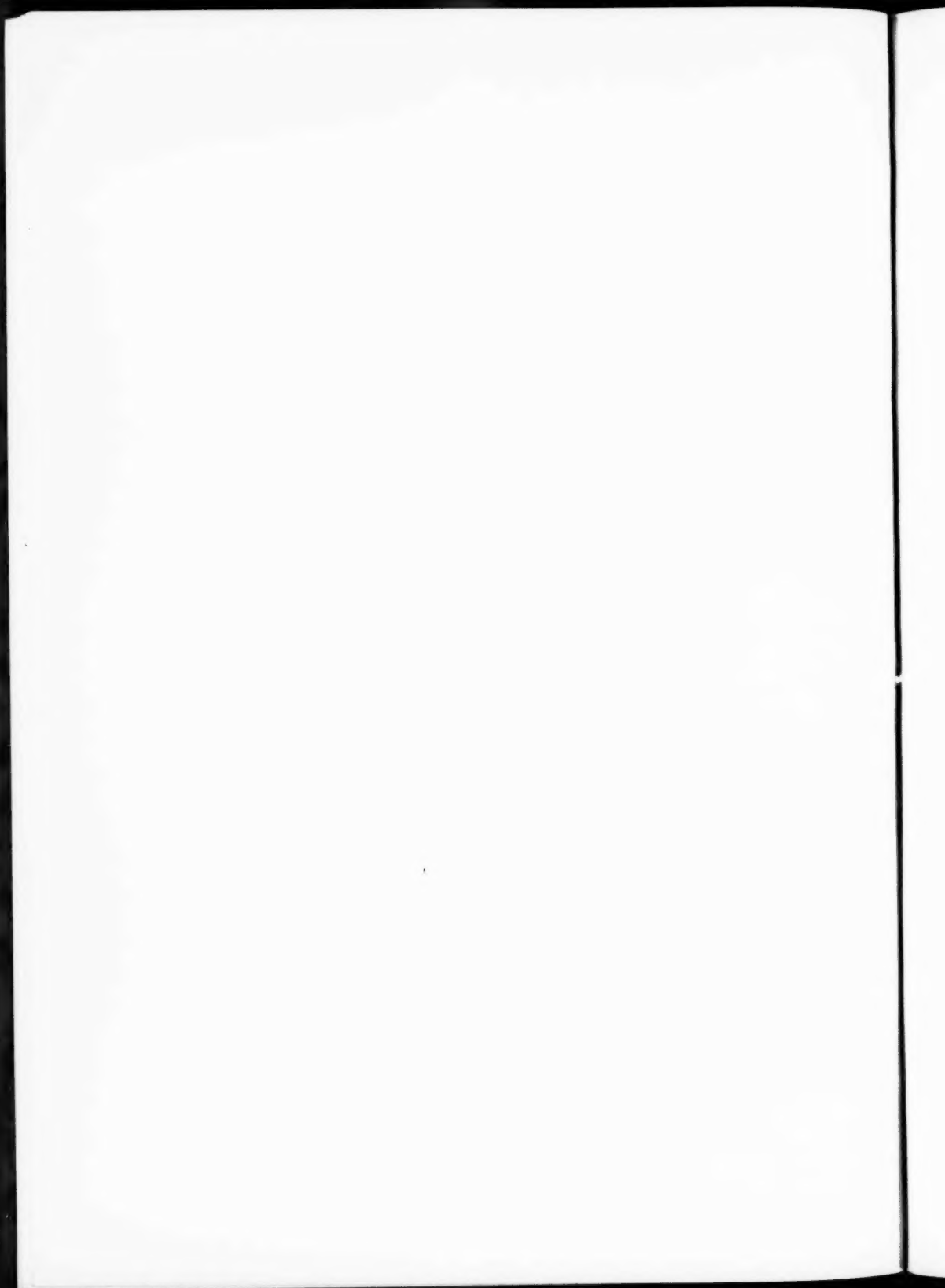




Latimeria chalumnae Smith.

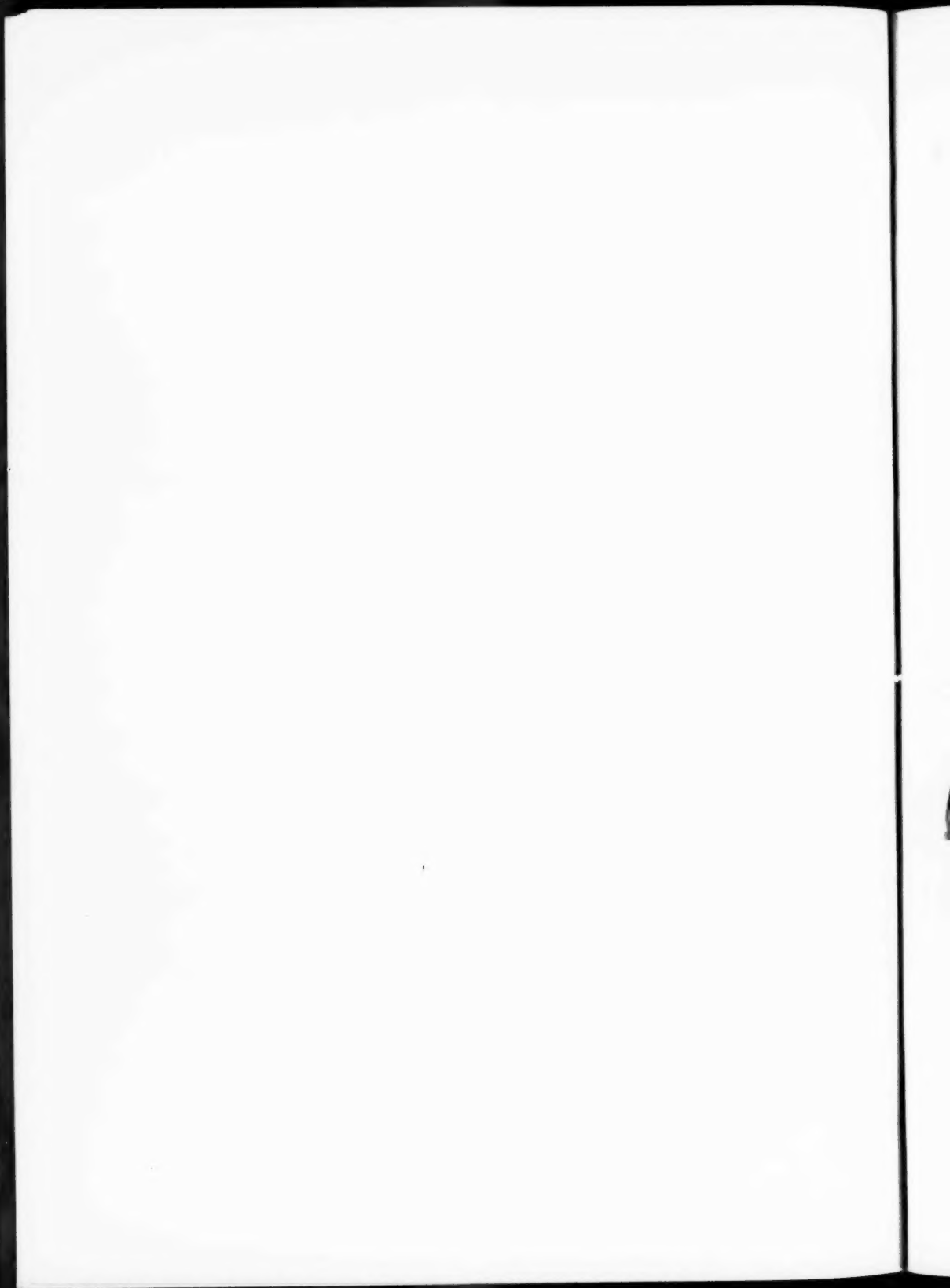
Above : Section through second rostral plate (90), $\times 12$. Anterior margin to the left. The outline below the small arrows is exposed outside the skin.

Below : Lateral view of postspiracular ossicle (51), $\times 3.8$. Anterior margin to the left.



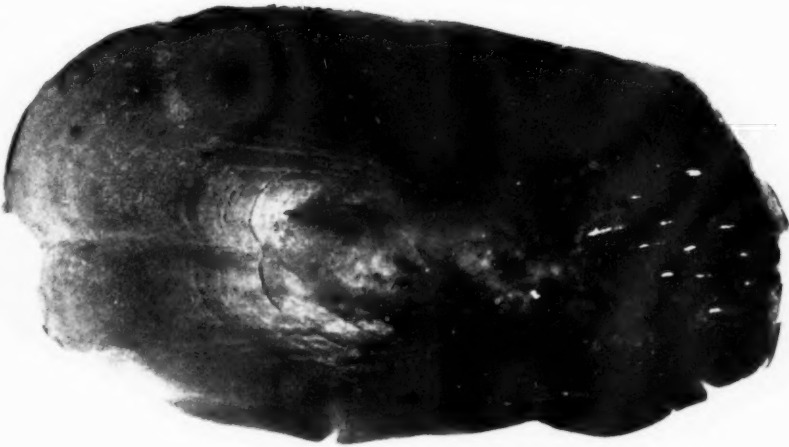


Lottimaria chalumnae Smith.
71. 8th row above lateral line below 9th caudal ray (dorsal), 43.
72. 10th row below lateral line above 6th caudal ray (ventral), 34.
See Folder-page II at end.



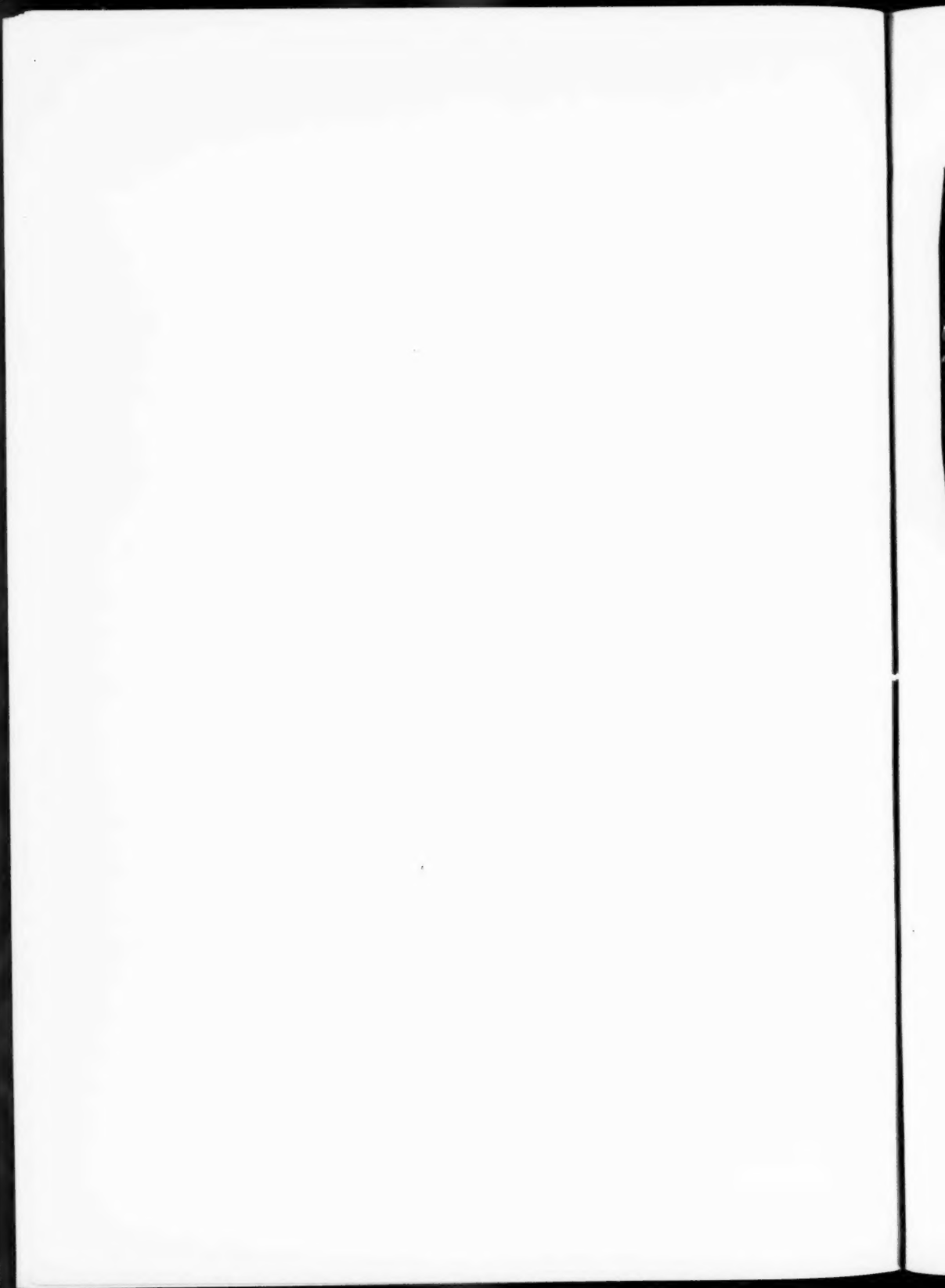


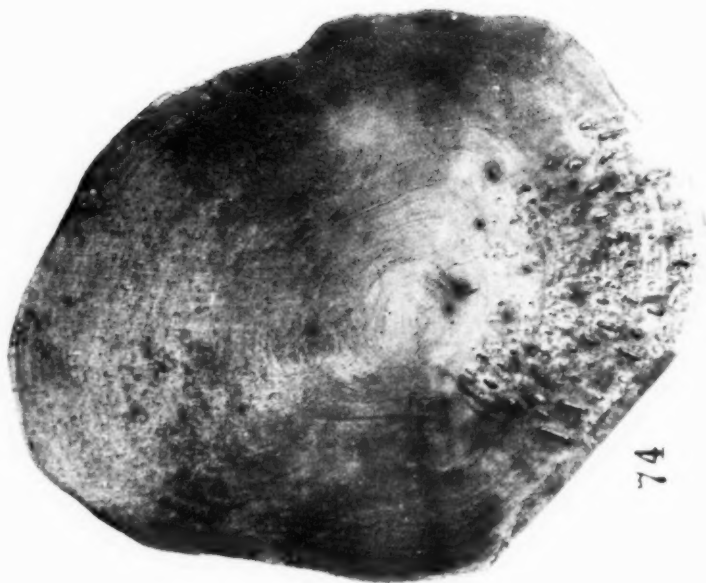
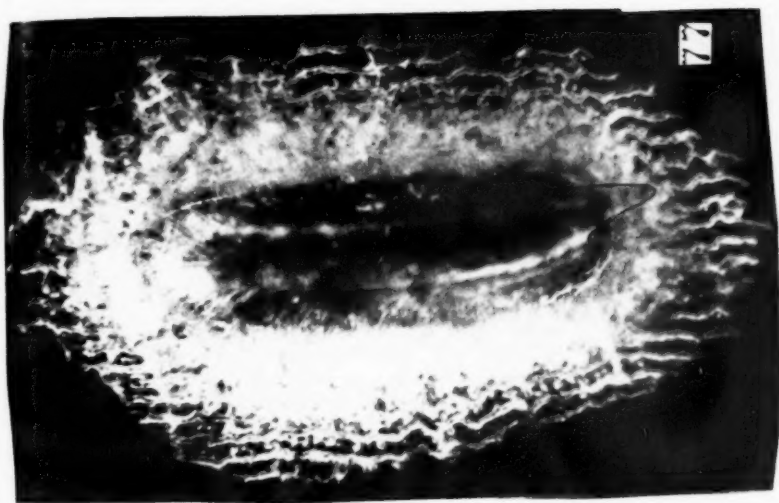
65



66

Latimeria chalumnae Smith.
65, 64th lateral line scale, $\times 43$. 66, 51st lateral line scale, $\times 3$.
See Folder, page II at end.



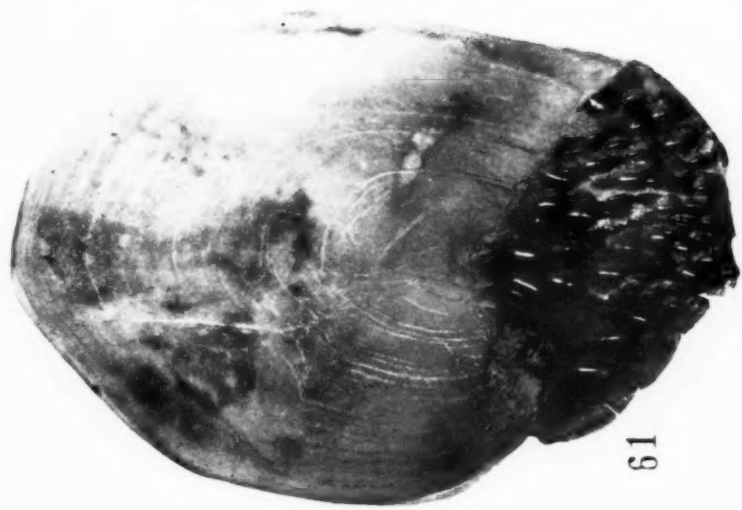


Lutjanus chalumnae Smith.

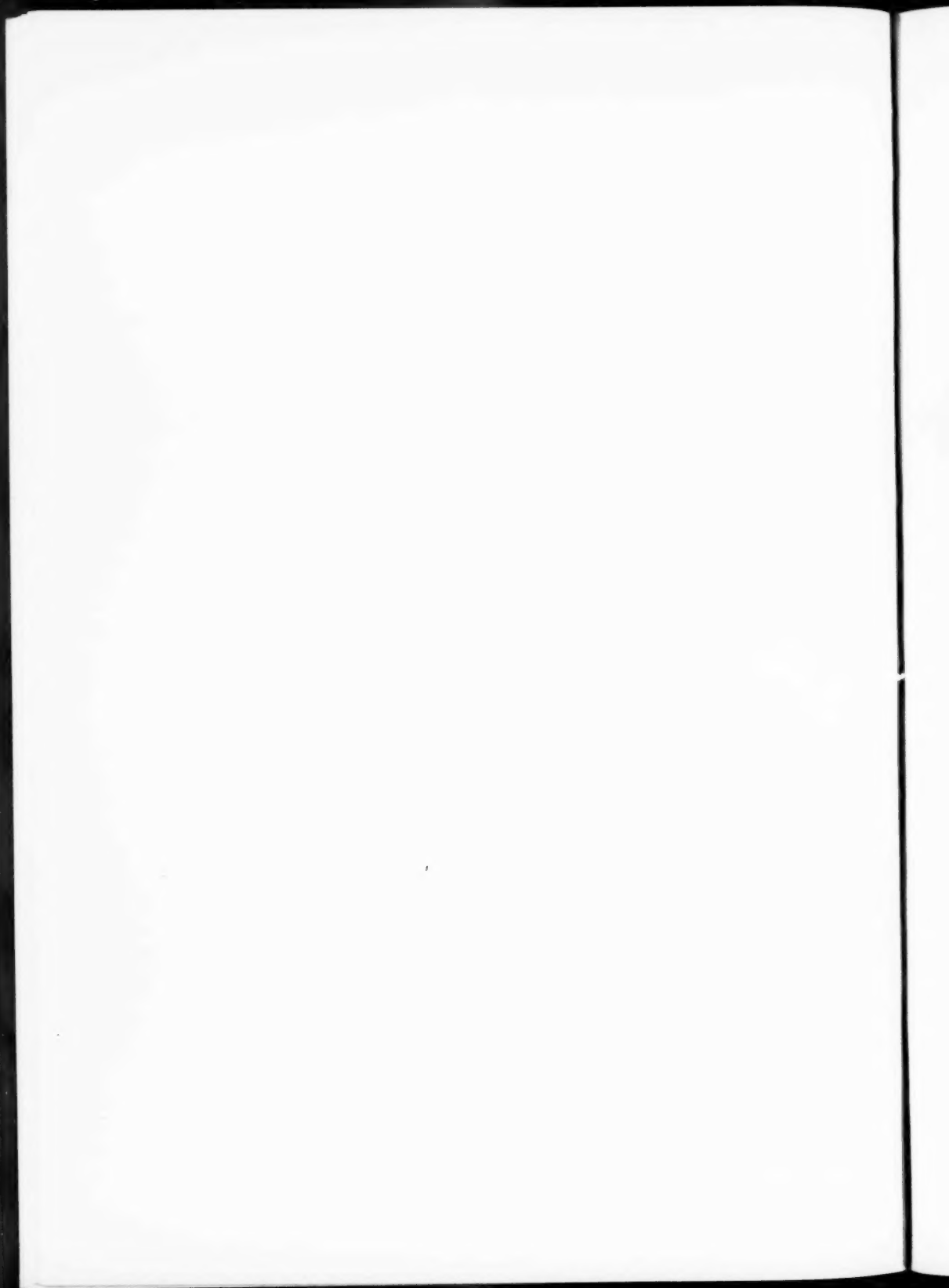
74. Upper outer surface of pectoral peduncle, $\times 64$.

77. Tubercle from scale on caudal peduncle below anterior rays. $\times 75$.

See Folder page II at end.

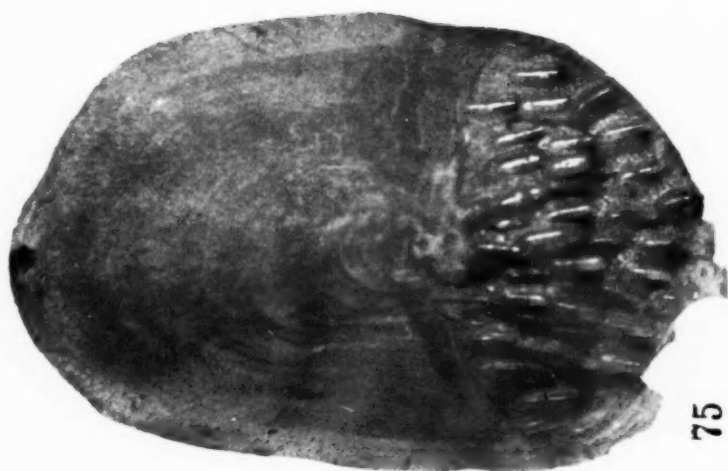


Letimaria chalumnae Smith.
61. Base of second dorsal (right side), $\times 2.2$. 69, 4th row above lateral line, interdorsal, $\times 3.2$.
See Folder-page II at end.



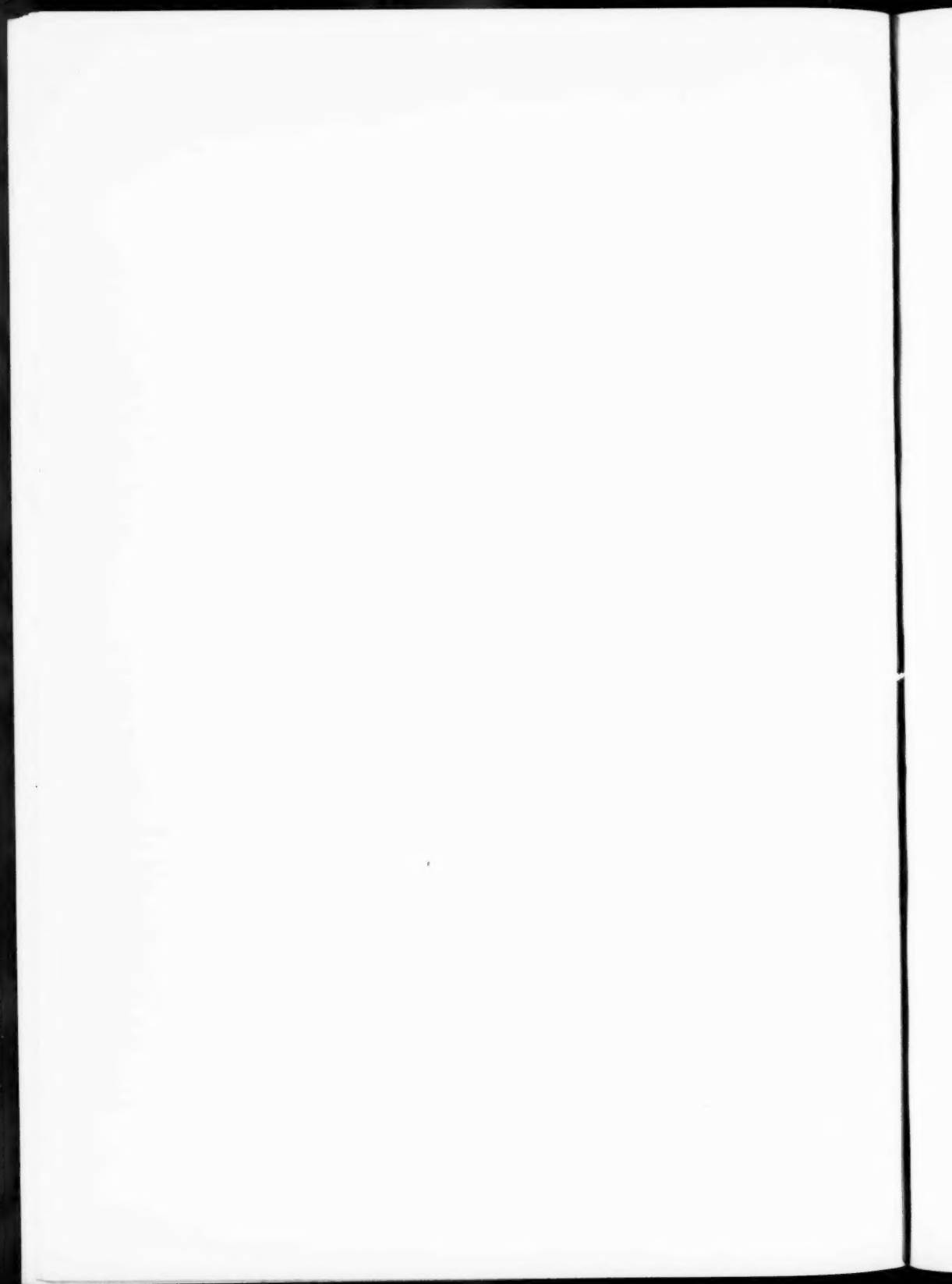


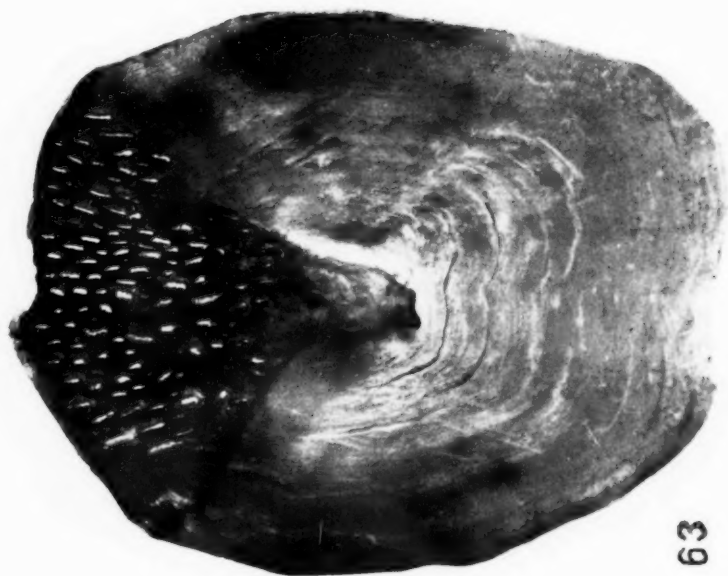
67



75

Letimoria chalumnae Smith.
75, Anterior surface of anal peduncle, $\times 6.4$. 67, 88th lateral line scale, $\times 10.2$.
See Folder-page II at end.

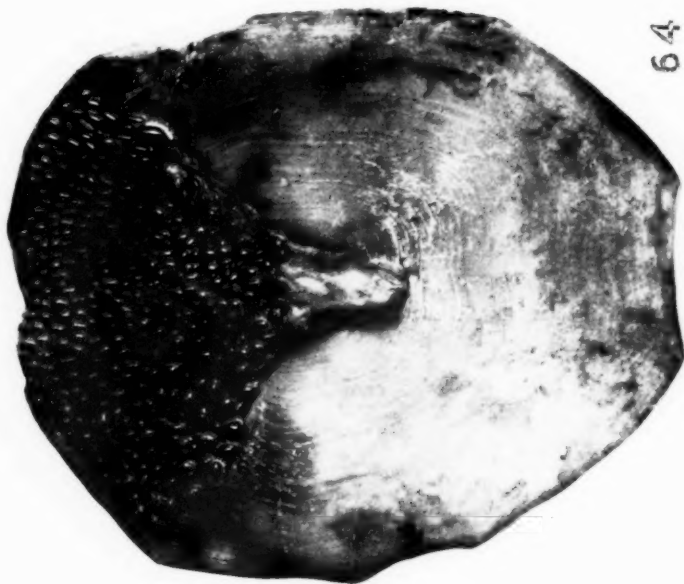




63

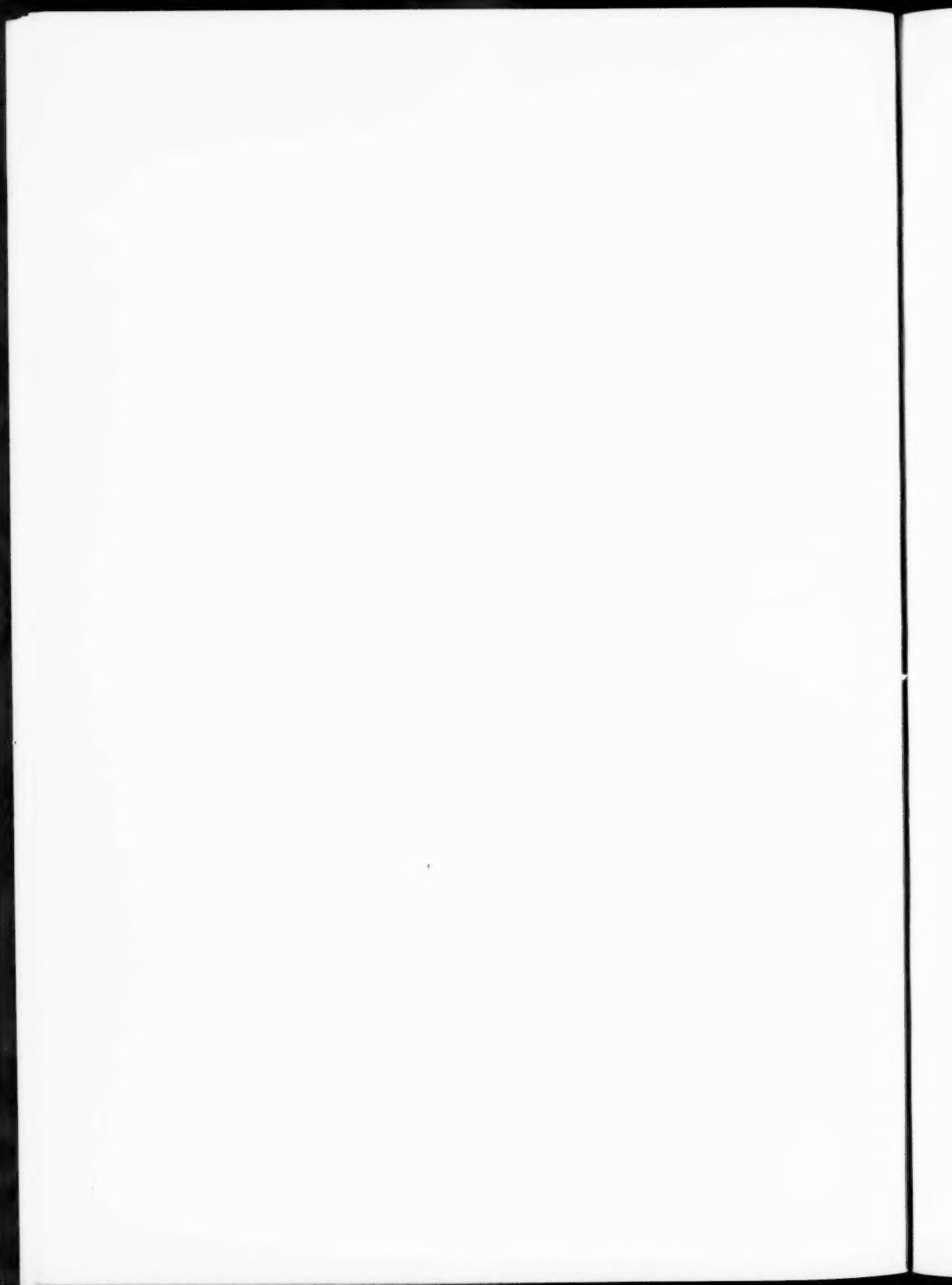
J. L. B. Smith.

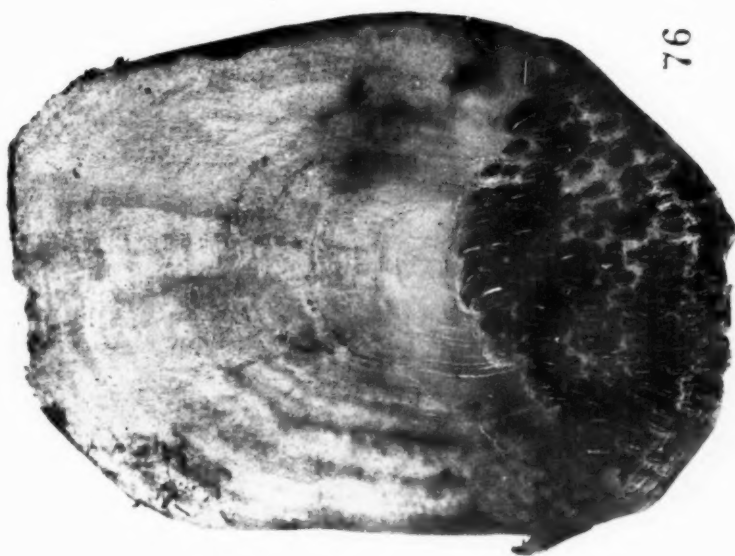
Neill & Co., Ltd.



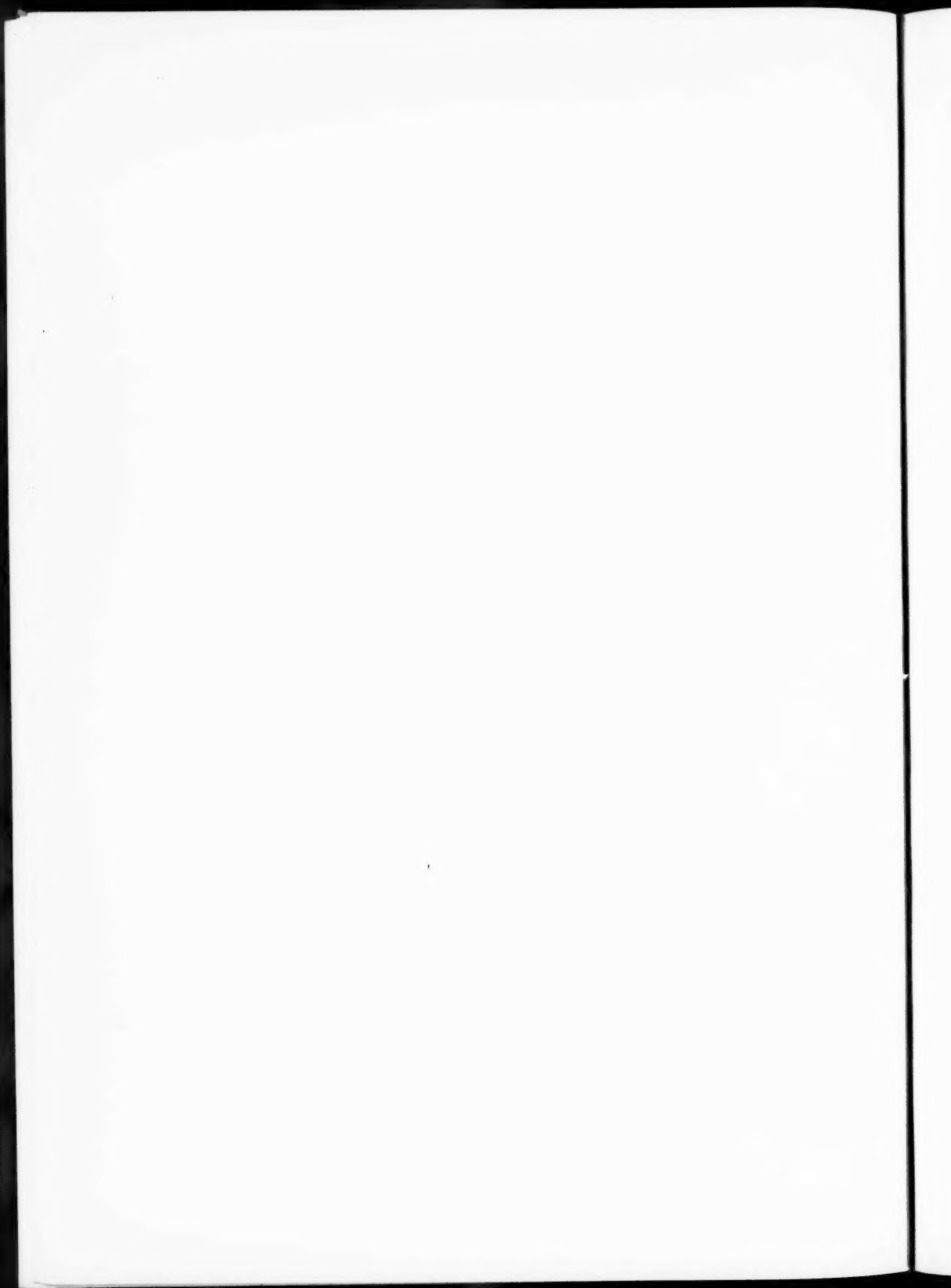
64

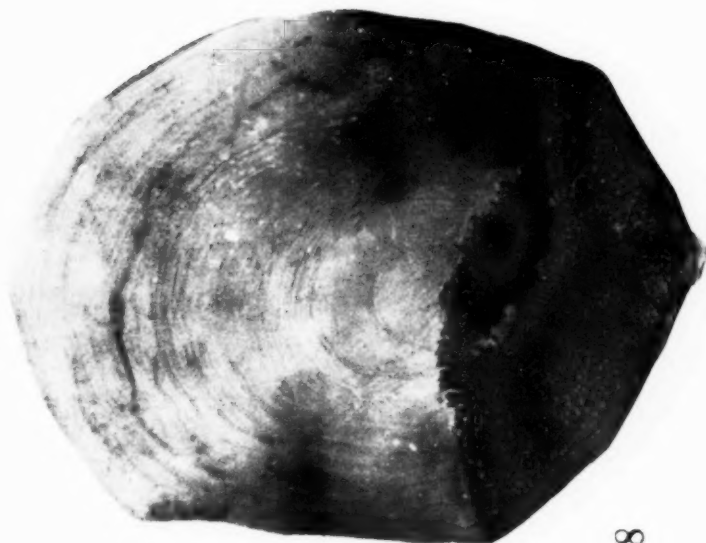
Lottimaria chalumnae Smith.
63, 18th lateral line scale, x 24, 64, 34th lateral line scale, x 24.
See Folder-page II at end.



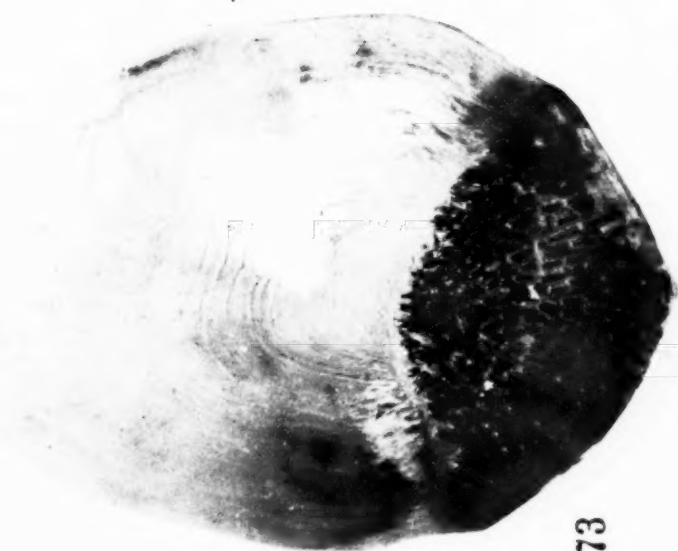


Littoraria chalumnae Smith.
76. Ventral anterior breast, $\times 2.5$. 70. 4th row above lateral line, behind second dorsal, $\times 2.7$.
See Folder-page II at end.



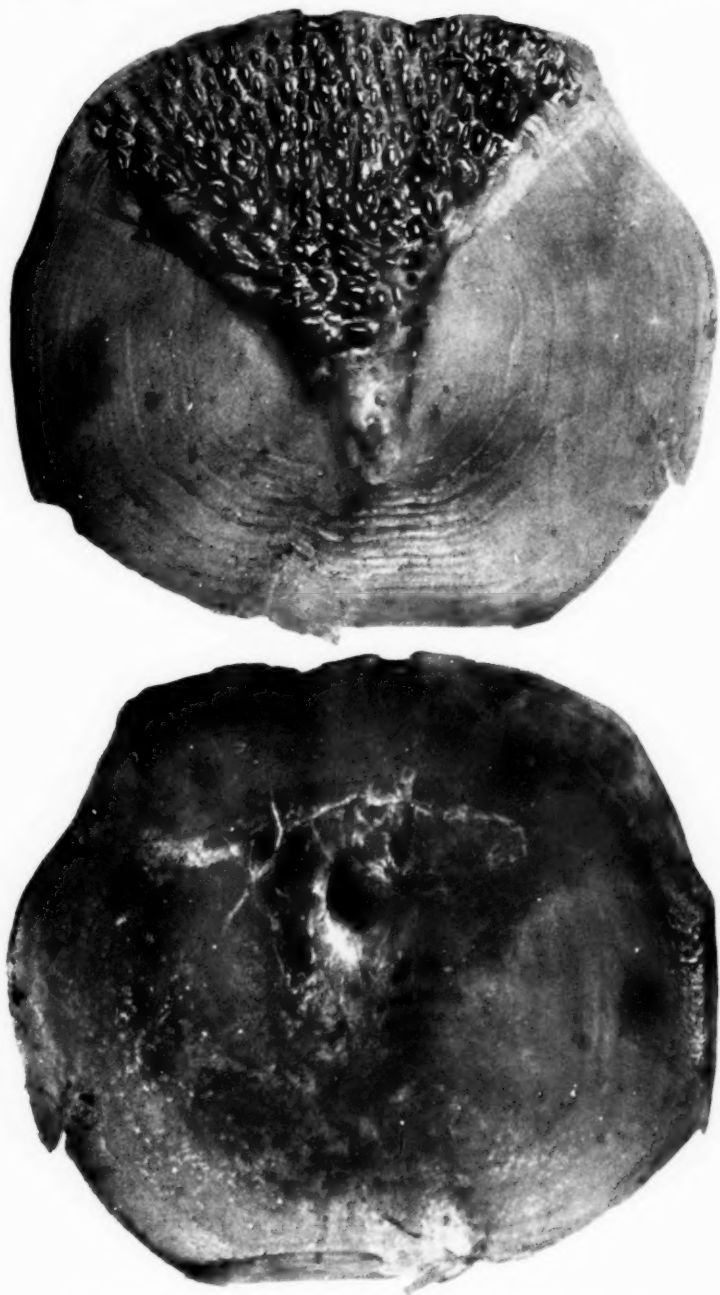


68



73

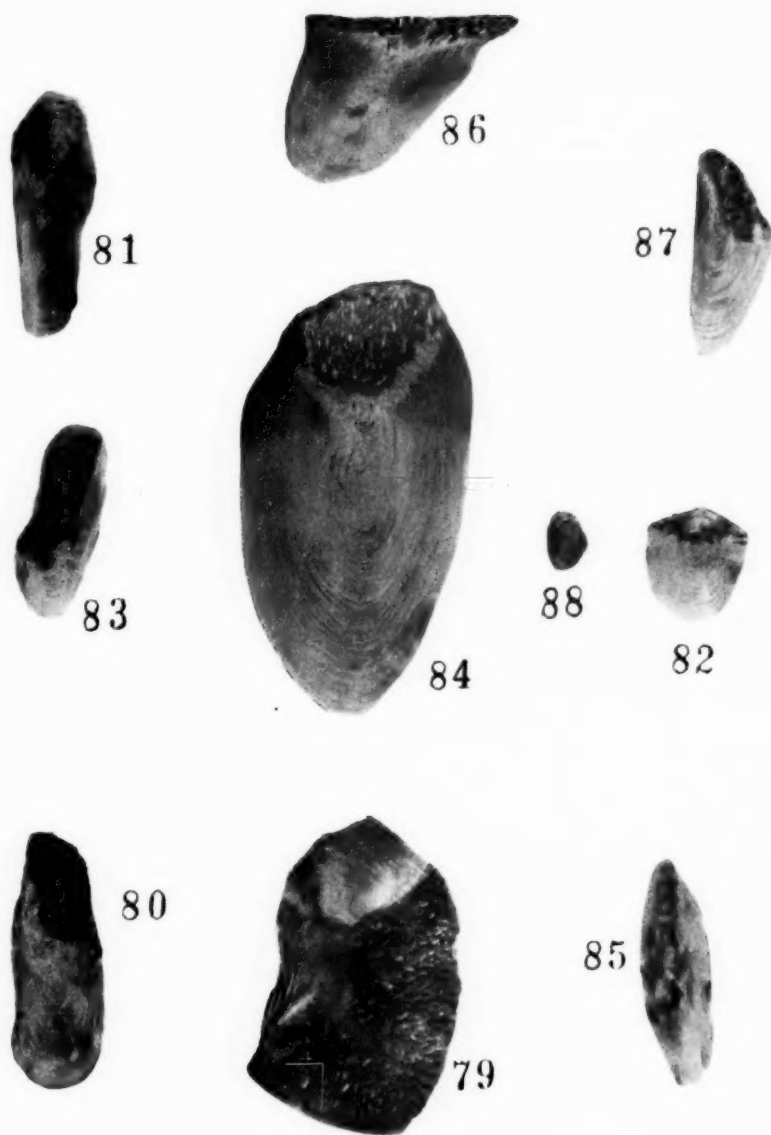
Littoraria chalcidensis Smith.
73. 7th row below lateral line, behind pelvic base. = 23.
68. 5th row below lateral line, behind pectoral base. = 24.
See Folder-page II at end.



Latimeria chalumnae Smith. Ninth lateral line scale from left side, $\times 3$.
Above: upper surface. Below: lower surface. Posterior margin of scale above.

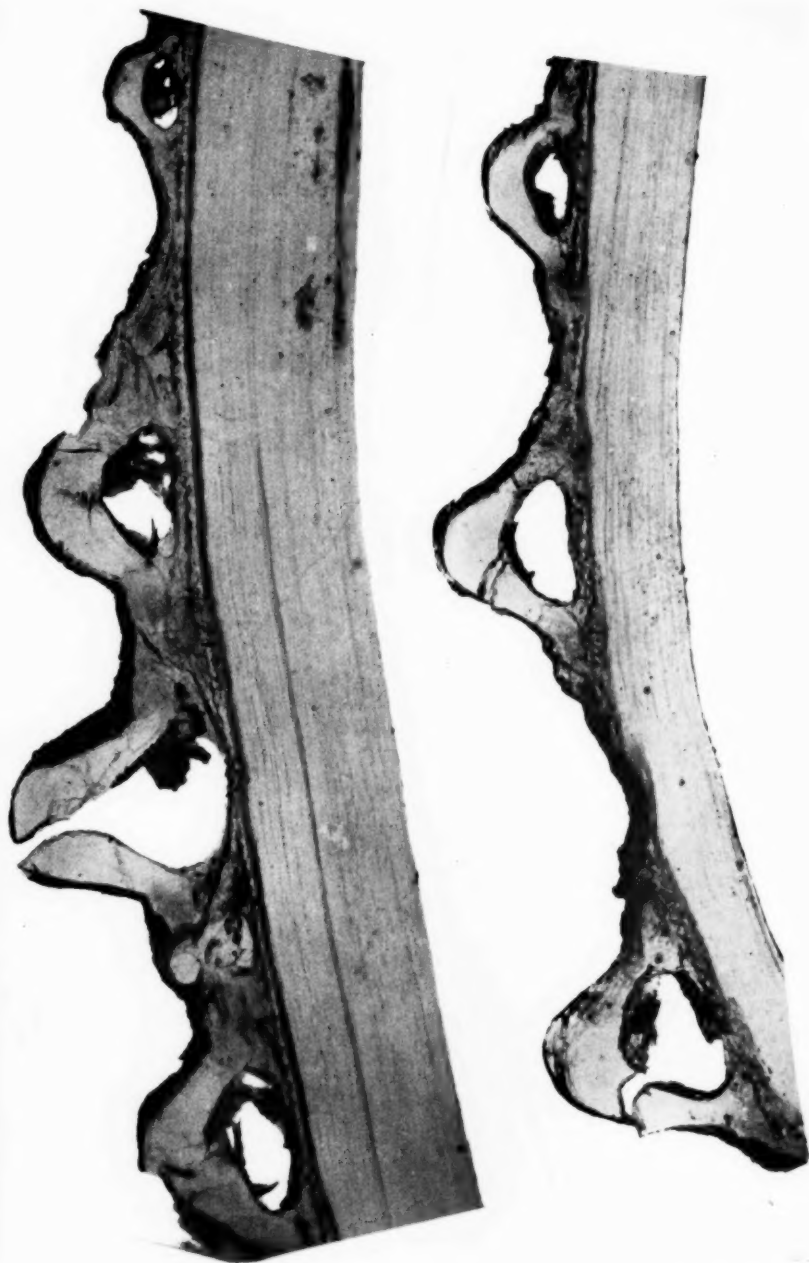
J. L. B. Smith.

Neill & Co., Ltd.



Latimeria chalumnae Smith.

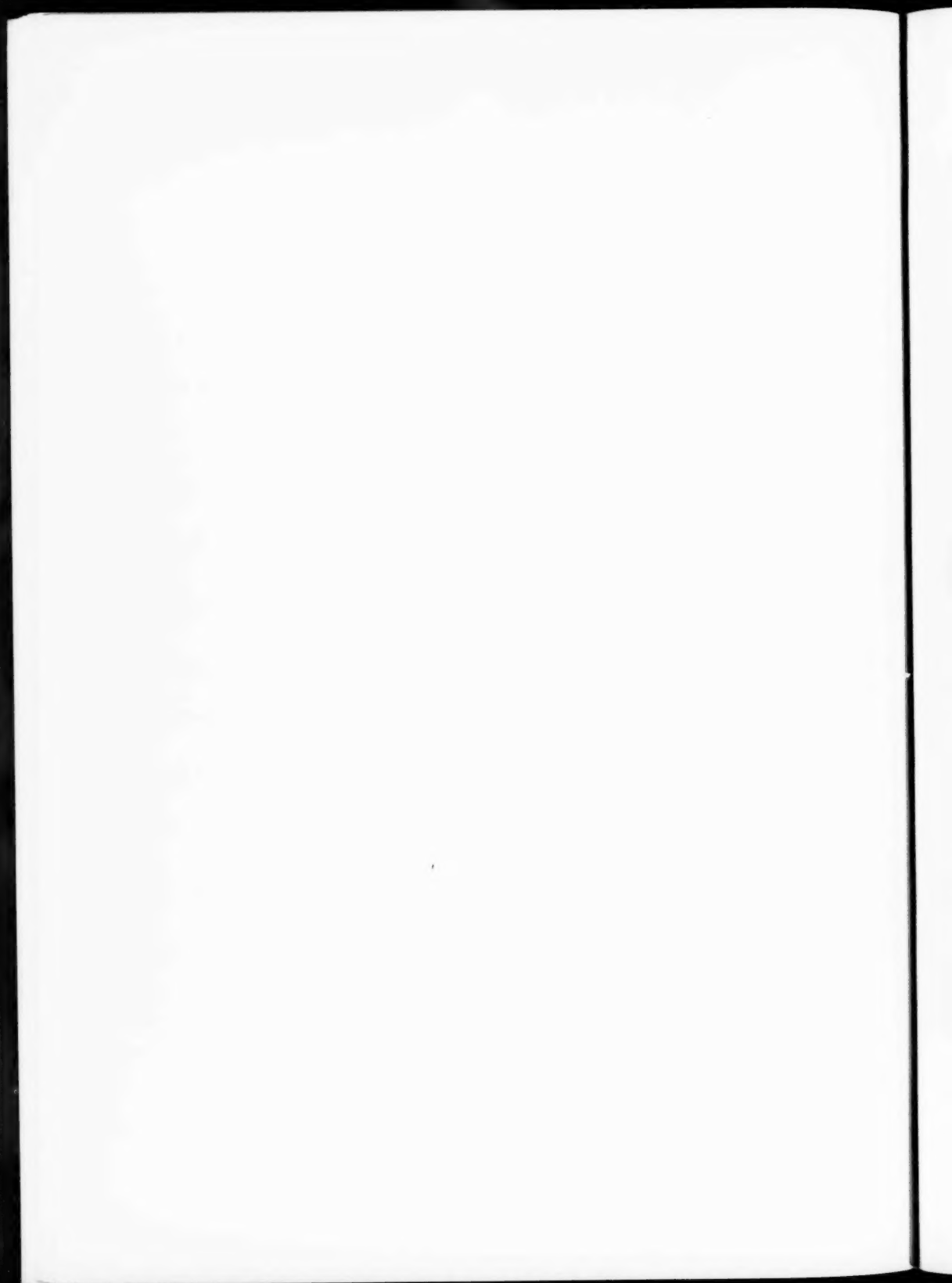
Scales: All $\times 14$. See Folder-page II at end.



Latimeria chalumnae Smith.
Sections of a scale from the upper portion of the caudal peduncle (78). Upper $\times 65$; lower $\times 48$.
See Folder-page II at end.

J. L. B. Smith.

Nell & Co., Ltd.





Lynx pardus Smith.
Section of skin from cheetah, $\times 75$. Outer surface above.

J. L. B. Smith.

Neill & Co., Ltd.



FOLDER-PAGE I.

Key to Plates and Text-figures.

OSSIFICATIONS.

1. Frontal.
- 1'. "Alisphenoid."
2. Frontal.
3. Fronto-nasal.
4. Postrostral.
5. Naso-antorbital.
6. Rostro-nasal.
- 7, 7'. Rostral.
8. Meso-rostral.
- 9, 10. Rostral.
- 11, 12, 13, 14, 15, 16. Parafrontal.
17. Parafronto-antorbital.
18. Latero-rostro-nasal.
19. Rostral.
20. Inner-rostral.
21. Mid-rostral.
22. Outer-rostral.
23. Postorbital.
24. Squamosal.
25. Preopercular.
26. Interopercular.
27. Subopercular.
28. Opercular.
29. Angular.
30. Splenial.
31. Gular.
32. Articular.
33. Pterygoid.
34. Quadrate.
35. Metapterygoid.
36. Ectopterygoid.
37. Autopalatine.
- 37'. Autopalatine dental plate.
38. Ectethmoid.
39. Symplectic.
40. Precoronoid.
41. Coronoid.
42. Antotic process of basisphenoid.
43. Articular-prearticular.
44. Dentary.
- 44'. Dental plates of dentary.
45. Copula.
46. Labial tooth plate.
47. Quadrato-jugal.
48. Lacrimo-jugal (suborbital).
49. Intertemporal.
50. Supratemporal.
- 50'. Inferior antorse process of the supratemporal.
51. Postspiracular.
52. Parasphenoid.
- 52'. Dental plate of parasphenoid.
53. Prevomer.
- 53'. Dental plate of prevomer.
54. Entopterygoid.
55. Inter-extrascapular.
56. 1st extrascapular.
57. 2nd extrascapular.
58. 3rd extrascapular.
59. Outer-extrascapular.

60. 1st lateral line scale.
- 61-88. Scales (see Folder-page).
89. Suprapterygoid denticulate.
90. Rostral dental plates.
91. Postrostral dental plate.
92. Prootic ossicle.
93. Prootic.
94. Hyomandibular ossification.
- 94'. Hyomandibular upper ear.
- 94". Hyomandibular lower ear.
95. Bony stud on nape.
96. Basisphenoid.
97. Cleithrum.
98. Clavicle.
99. Extracleithrum.
100. I. Articulation facet for
II. Articulation facet for
III. Articulation facet for

OTHER STRUCTURES.

- A. Rostral narial aperture and
- B. Lower lateral narial aperture.
- C. Upper lateral narial aperture.
- D. Rostral papilla.
- E. Olfactory capsule.
- F. Spiracle.
- G. Pseudo-maxillarial fold.
- H. Hyoidean gill-slit.
- J. Tube, foramen, or sheath for
V and VII nerves.
- K. Cartilage.
- L. Olfactory lobes of the brain.
- M. Brain cavity.
- N. Eye.
- O. Adductor fossa.
- P. Muscle.
- Q. Branchial arches (I-IV).
- R. Ethmoidal nasal cavity.
- S. Skin.
- T. Lateral spiracular groove.
- U. Spiracular pouch.
- V. Antotic cavity.
- W. Palatine canal.
- X. Mandibular labial fold.
- Y. Dentate skin fold from hyomandibula.
- Z. Median ridge from clavicle.

SENSORY

- a. Parafrontal canal.
- b. Infraorbital canal.
- d. Jugal canal.
- e. Mandibular canal.
- f. Supratemporal canal.
- g. Rostral commissural canal.
- h. Posterior rostral commissural canal.
- g. Preopercular canal.
- r. Fronto-rostral commissural canal.
- t. Supratemporal commissural canal.

ures.

-page II).
iculate area.
ate.

ication.
er cartilage.
er cartilage.

et for ceratohyal on basihyal.
et for urohyal on basihyal.
et for basibranchial on basihyal.

R STRUCTURES.

re and tube.
perture and tube.
perture and tube.

ld.
eath for ophthalmic branches of the
e brain.

V).
ty.
bove.

ld.
n hyomandibular.
avicle articulation to symphysis.

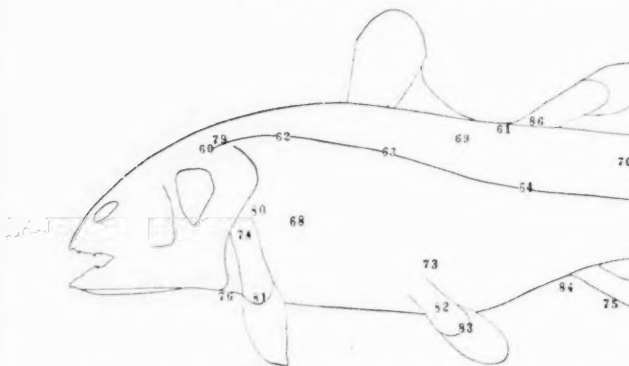
RY CANALS.

canal.
missural canal.
ssural canal.
missural canal.

FOLDER-PAGE II.

SCALES.

Key to Plates XXXII-XLII in

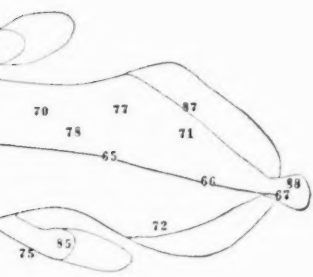


TEXT-FIG. 20.—*Latimeria chalumnae* Smith. To show the approximate positions of the scales. Unless otherwise stated, scales are from the left side.

- 60. 1st lateral line.
- 61. Base, 2nd dorsal, right side.
- 62. 9th lateral line.
- 63. 18th lateral line.
- 64. 34th lateral line.
- 65. 51st lateral line.
- 66. 64th lateral line.
- 67. 88th lateral line.
- 68. 5th row below lateral line, behind pectoral.
- 69. 4th row above lateral line, interdorsal.
- 70. 4th row above lateral line, behind second dorsal.
- 71. 8th row above lateral line, below 9th caudal.
- 72. 10th row below lateral line, above 6th caudal.
- 73. 7th row below lateral line, behind pelvic.
- 74. Upper lateral face of pectoral limb.
- 75. Anterior face of anal peduncle.
- 76. Anterior mid-breast.
- 77. Tubercle from scale below dorsal caudal.
- 78. Sections of scale from above lateral line.
- 79. 2nd lateral line.
- 80. Axil of pectoral.
- 81. Base of mid-rays of pectoral.
- 82. Middle of dorsal face of limb of pelvic.
- 83. Base of mid-rays of pelvic.
- 84. Mid-ventral, just anterior to anal insertions.
- 85. 3rd scale up from base of mid-rays of anal.
- 86. 2nd dorsal base, lateral.
- 87. Base of dorsal, 9th principal caudal ray.
- 88. Dorsal end of supplementary caudal.

II.

I inclusive.



approximate positions from which
seen.
left side of the fish.

pectoral base.
anal.
second dorsal.
h caudal ray.
h caudal ray.
pelvic base.

caudal rays.
line on peduncle.

vic.

insertion.
of anal.

ray.
l.

A METHOD OF CORRECTING AN OBJECTIVE NOISE METER FOR USE ON COMPOSITE TONES.

By R. GUELKE, Ph.D.

(Communicated by B. L. GOODLET.)

(With ten Text-figures.)

(Read March 15, 1939.)

CONTENTS.

	PAGE		PAGE
I. INTRODUCTION	107	IV. THE PEAK/R.M.S. RATIO AS AN INDICATION OF THE CORRECTION REQUIRED	113
II. THE DIFFERENCES BETWEEN THE INDICATIONS OF A CONVENTIONAL OBJECTIVE NOISE METER OR SOUND LEVEL METER AND THE EQUIVALENT LOUDNESS	108	V. PRACTICAL CONSTRUCTION OF AN INSTRUMENT USING THE PEAK/R.M.S. RATIO TO CORRECT FOR COMPOSITE TONES.	120
III. METHODS OF CORRECTING THE CONVENTIONAL OBJECTIVE NOISE METER	112	VI. ACKNOWLEDGMENTS	122

I. INTRODUCTION.

Loudness is now always measured in terms of the International Phon (which is identical with the B.S. Phon). The phon is defined as a measure of "equivalent loudness." A sound has an equivalent loudness of x phons if a "standard observer" (in practice a number of observers) considers the sound under test to be equal in loudness to a plane sinusoidal wave having a frequency of 1000 cycles per second and an R.M.S. pressure of x decibels above $\cdot 0002$ dyne per square cm. (the 1000-cycle source being situated directly facing the observer).

A noise-measuring apparatus is generally divided into two types, subjective and objective. In the former type of instrument, a source of sound of variable intensity is adjusted until it is judged to be of equal loudness to the noise being measured. In the latter, a microphone and amplifier are used with a weighting network to simulate the response curve

of the ear. The output from the amplifier is then measured, and is regarded as a measure of the loudness of the noise received by the microphone. This, however, has been found to be liable to considerable error.

Subjective noise meters of the latest type give results which are mainly independent of the type of noise which is being measured.* The results, however, depend on the judgment of the individual taking the measurement. The ear is very insensitive to slight changes in intensity, and because of the difficulty of comparing different types of sound the spread of individual measurements is large. If reasonably accurate measurements are required, it is therefore necessary for a number of observers to measure the noise independently and to take the average of the results. The disadvantages of subjective noise meters are:

- (1) For reliable measurement a number of observers are required.
- (2) Sustained noises only can be measured.
- (3) Unless independent observers are available the individual measurements may be biased.
- (4) It is not possible to obtain a continuous record over a period.

Objective noise meters do not have these disadvantages, but the type generally available does not give readings which are independent of the type of noise. Thus, if a meter is constructed consisting of a microphone, amplifier, weighting network, and output meter, and if the instrument is adjusted to read correctly for pure tones of all frequencies, it may read as much as 24 phons low, relative to a determination by the standard method described in the first paragraph, for certain types of noise over certain ranges of intensity.

At present it is necessary to use either subjective or objective noise meters according to the circumstances and possibilities of each individual case. For greater accuracy a subjective meter is generally preferred, whereas for measurements of noises of a known type or for any of the contingencies mentioned above, objective meters of conventional type are employed.

II. THE DIFFERENCES BETWEEN THE INDICATIONS OF A CONVENTIONAL OBJECTIVE NOISE METER OR SOUND LEVEL METER AND THE EQUIVALENT LOUDNESS.

The quantity measured by a sound level meter or objective noise meter of the conventional type will be referred to as the "equivalent energy" †

* B. G. Churcher and A. J. King, *J.I.E.E.*, vol. lxxxi, 1937, p. 57.

† According to American Tentative Standards Z.24.3, 1936, such a meter is referred to as a "Sound Level Meter" and the indications as "Sound Level Decibels."

of a noise. This designation is only strictly correct if the output meter employed on the instrument is of the R.M.S. type (*i.e.* electrostatic, thermojunction, or hot-wire type). Instruments using a rectifier type of output meter give readings sufficiently close to the equivalent energy to be included in this group.

The equivalent energy differs from the equivalent loudness of a complex tone. The amount of this difference has been determined by Fletcher and Munson,* and more recently by Churcher and King (*loc. cit.*).

Consideration of the results obtained has shown in both papers that they can be explained by the following theory.

According to the resonance theory of hearing, a complex sound, consisting of a number of pure tones, is analysed in the ear by means of a number of mechanical resonators. Each individual resonator sends a stimulus to the brain creating sensations of pitch and loudness. If the stimulus from each resonator were proportional to the energy received by that resonator, then the sensation of loudness would be equal to the total equivalent energy of the sound. If that were so, a conventional objective noise meter would give a correct reading for all types of noise.

It has been shown, however, that the energy-sensation relation is not a linear one, consequently a sound consisting of a number of pure tones will not have the same equivalent energy as a single pure tone of equal loudness. Whatever the relation between energy and sensation, the largest discrepancies between the equivalent loudness and the total equivalent energy will be obtained for sounds consisting of a large number of pure tones of equal loudness. In order to determine the amount of this deviation, sounds consisting of two tones and six tones in both harmonic and non-harmonic relationships were measured by the standard technique and by an "equivalent energy meter." The results of these measurements are given in fig. 1. A sound produced by a relaxation oscillation was also measured, because such a sound can be regarded as requiring a comparatively large correction. It consists of a large number of components when analysed in a Fourier series. These measurements were taken for sounds over a large range of intensity, as represented in fig. 1.

Fig. 2 shows the stimulus-sensation relation which was deduced from these measurements by Gates (see the discussion to first reference). The relationship between the correction required, the "equivalent energy," and the number of equally loud pure tones is shown in fig. 1. The values deduced from the relationship of fig. 2 are drawn as solid curves. It can be seen that the measurements agree well with the calculation from the stimulus-sensation curve of fig. 2.

From these facts it would appear possible to apply a correction to

* Fletcher and Munson, J.A.S.A., vol. v, 1933, p. 82.

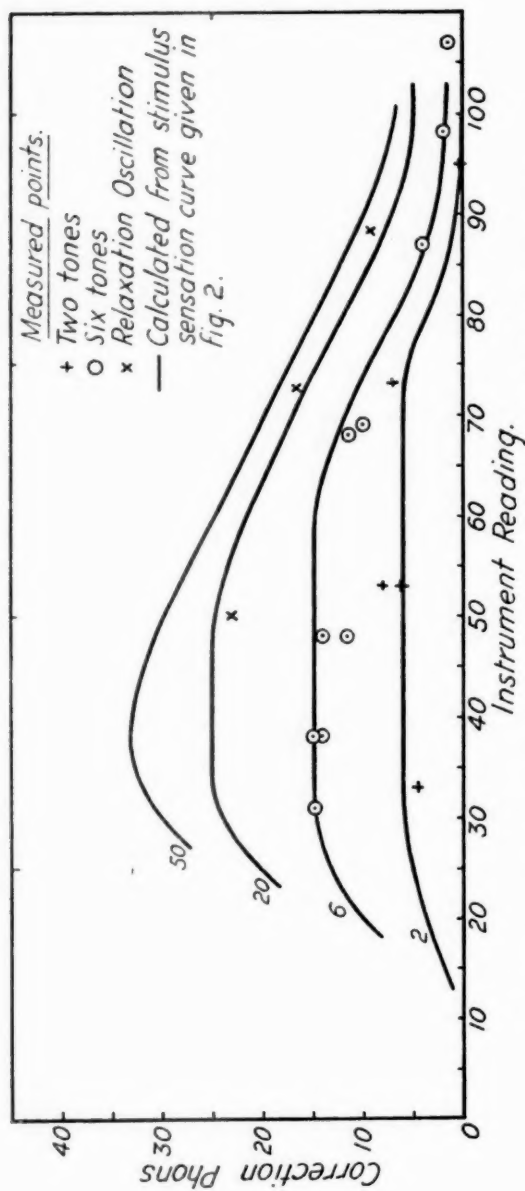
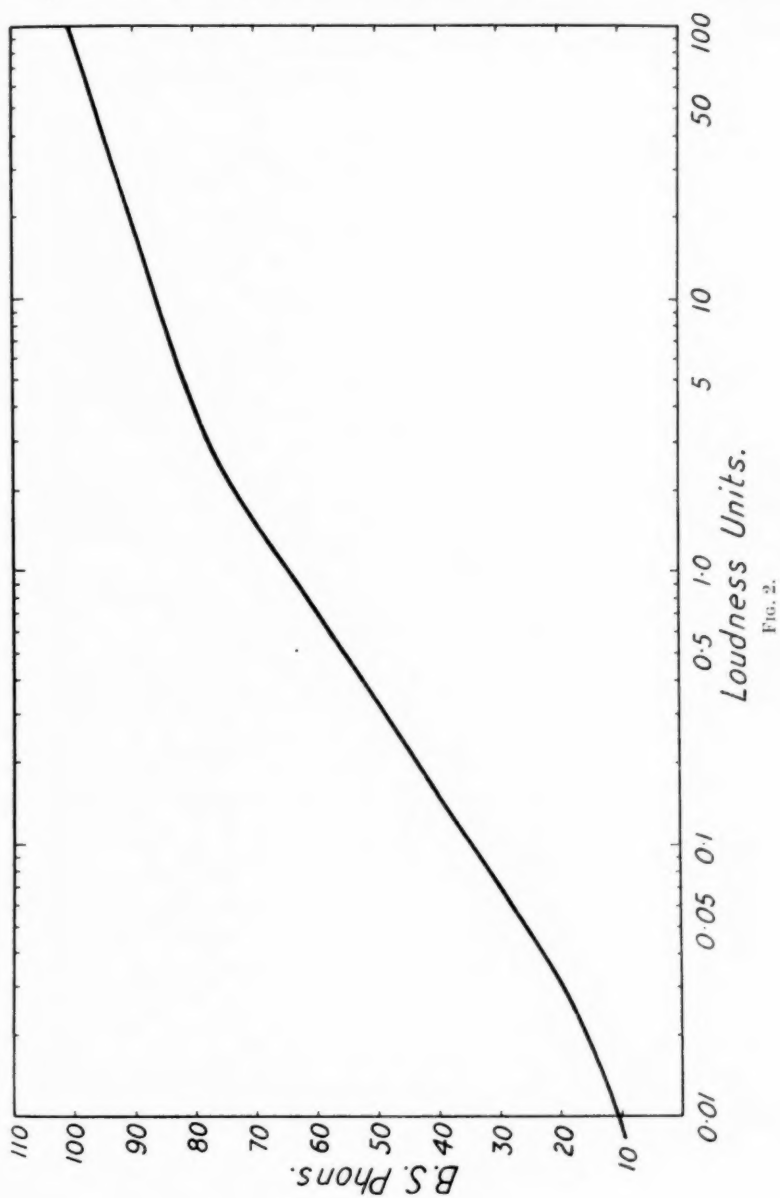


FIG. 1.—Correction curve for objective noise meter for noises consisting of 2, 6, 20, and 50 pure tones.



the equivalent energy in the case of sounds consisting of pure tones of equal loudness—this correction to depend only on the number of tones. Consideration of the masking effect of tones which are close together in frequency show that such a correction is not independent of the frequency relationship between the individual tones.

The correction required is therefore dependent on:

- (1) The number of constituent pure tones.
- (2) The relative loudness of these tones.
- (3) The frequency relation between the constituent tones.

It was noted above that the maximum correction was to be expected with a number of tones of equal loudness. If this case is catered for, it is possible that the intermediate cases will be somewhere near the correct value.

The effect of masking is only noticeable at high intensities. At high intensities, however, the corrections required are small; a neglect of masking effects will therefore not be of great consequence at these intensities. At low intensities, on the other hand, the masking effects are only noticeable when the individual tones are so close to each other in frequency as to cause audible beats, which are sufficiently slow to cause recognisable loudness variations.

It would be possible to construct an objective noise meter which would give readings approximately in accord with the primary standard if some method were found of determining the number of constituent tones in a sound. This principle has been used in the development of the instrument described below.

A totally different method of attack was suggested by Steudel,* which involves a different theory of the action of the ear. One consequence of this theory would be that loudness variations of 10 phon should be obtained by altering the phase relationships of a fundamental and second harmonic at all intensities. Experiments made by the author have failed to detect such an effect. Bürok, Kotowski, and Lichte † have also shown that Steudel's experimental results can be explained by the resonance theory with the help of a Fourier analysis of the noises investigated.

III. METHODS OF CORRECTING THE CONVENTIONAL OBJECTIVE NOISE METER.

To be able to apply the corrections given in fig. 1, it is first necessary to find some method of determining the number of constituent pure tones. The accuracy required must always be considered, and it should be noted

* U. Steudel, *Zs. f. Hochfrequenztech u. Electro-akustik*, vol. xlv, 1933, p. 116.

† E. Bürok, P. Kotowski, and H. Lichte, *E.N.T.*, vol. xii, 1935, p. 278.

that in sound measurement the accuracy required is not great. Both American (*loc. cit.*) and German specifications* for sound level meters allow a tolerance of ± 3 db. which on an energy basis is equivalent to +100 per cent. or -50 per cent. That this accuracy is sufficient can be justified by regarding the extremes of individual judgments. With people of perfectly normal hearing, discrepancies of ± 6 db. between individuals occur frequently when comparing sounds of different types. If it were therefore possible to determine the correction to an accuracy of ± 3 db. it could be regarded as satisfactory.

It will be assumed in the following that the output of a sound level meter is available, and that the meter is correctly weighted to correspond with the sensitivity curve of the ear at the intensity level under investigation.

An ideal solution would be to have a number of resonators equal in number and response to the resonators in the ear. As there are probably about 24,000 resonators in the ear, it would obviously be impossible to construct such a large number of electrical resonating circuits, and mechanical resonators would be difficult to use over the wide frequency range required.

A possible compromise recommended by Thilo and Steudel† would be to use a limited number of filters. In order to allow for the fact that two tones may be found within the same filter, they recommend measuring the peak instead of the R.M.S. output from each filter. These peak outputs from each filter are then added according to the loudness relation.

IV. THE PEAK/R.M.S. RATIO AS AN INDICATION OF THE CORRECTION REQUIRED.

For some time it has been known that the measurement of the peak voltage instead of the R.M.S. at the output of an objective noise meter will tend to give more accurate results.‡ This is due to the fact that for alternating currents consisting of a number of components of different frequency there is a probability that the Peak/R.M.S. ratio will be higher than for a pure sine wave.

Because the equivalent loudness of a composite tone is greater than the equivalent energy, the fact that a peak meter usually gives a relatively higher reading on composite tones makes it possible to calibrate it in such a manner that it tends to approximate more nearly to the equivalent loudness than an equivalent energy meter.

* A.Z., vol. ii, 1937, p. 54.

† H. G. Thilo and U. Steudel, *Wiss. Veröff., a.d. Siemens Konz.*, vol. xiv, 1935, p. 78.

‡ H. Davis, J.I.E.E.

If the components form a harmonic series, the Peak/R.M.S. ratio of a composite noise depends to a great extent on the phase relationship of the individual components. The loudness, on the other hand, is independent of these phase relationships except at high intensities (Ohm's law of acoustics). Before accepting the peak reading as a measure of the loudness, it is therefore first necessary to ascertain whether the effect of phase is likely to be important.

It can be shown that a noise which gives rise to a wave of the form

$$V = \sin ut + \frac{1}{3} \sin 3ut + \frac{1}{5} \sin 5ut + \dots + \frac{1}{2n-1} \sin (2n-1)ut$$

at the output meter, would give a Peak/R.M.S. ratio approximating to 1. The Peak/R.M.S. ratio of a pure sine wave is 1.41. The Peak/R.M.S. ratio of this series is therefore smaller, whereas the assumption was that a composite tone should have a larger value.

Therefore, although the peak reading in some cases gives a value which is closer to the equivalent loudness than the R.M.S. reading, there are other cases in which the peak reading is of no assistance in improving the accuracy of the equivalent energy meter.

The difference between the peak reading and the R.M.S. reading, even when the phase relations are propitious, is not as large as the correction required; *e.g.* the maximum Peak/R.M.S. ratio obtainable with six tones of equal loudness is $\sqrt{2n}$, *i.e.* 3.46. This is equivalent to a correction of about 8 db., whereas the correction required at medium intensities is about 15 db. The ratio 3.46 is, however, only obtained in very exceptional circumstances; a more representative value would be about 2.6, and the correction obtained then would only be about 5 db.

The objections to using the peak reading as an indication of equivalent loudness are:

- (1) The gain in accuracy on composite sounds relative to the ordinary equivalent energy meter is not great.
- (2) Sounds consisting of harmonic series in certain phase relationships show the same discrepancies as the equivalent energy meter.

These objections can be removed in the following manner:—

- (1) Instead of reading on a peak meter directly, the Peak/R.M.S. ratio is determined.
- (2) The Peak/R.M.S. ratio is determined a second, third, and fourth time after shifting the phase of each component by an amount equal to $\frac{\pi}{2}$, π , and $\frac{3\pi}{2}$.

- (3) The maximum of these four Peak/R.M.S. ratios is chosen, and a correction is applied to the equivalent energy depending on this ratio and on the equivalent energy.

This reduces the possible errors due to phase relationships to within reasonable limits, and a suitably large correction can be applied dependent on the Peak/R.M.S. ratio.

It has been mentioned above that a series of the form

$$y = \sin x + \frac{1}{3} \sin 3x + \frac{1}{5} \sin 5x + \dots + \frac{1}{2n-1} \sin (2n-1)x \quad (1)$$

has a Peak/R.M.S. ratio approaching 1. If each term of this series is altered in phase by an amount equal to $\frac{\pi}{2}$ the series will change to

$$y = \cos x + \frac{1}{3} \cos 3x + \frac{1}{5} \cos 5x + \dots + \frac{1}{2n-1} \cos (2n-1)x \quad (2)$$

This series has a Peak/R.M.S. ratio of

$$\frac{\left(1 + \frac{1}{3} + \frac{1}{5} + \dots + \frac{1}{2n-1}\right) \sqrt{2}}{1 + \frac{1}{3^2} + \frac{1}{5^2} + \dots + \frac{1}{(2n-1)^2}}$$

The value of this expression will not concern us. What is important is that the cos series (2) gives the maximum possible Peak/R.M.S. ratio.

After changing each component by $\frac{\pi}{2}$, the series (1), instead of giving a Peak/R.M.S. ratio nearly equal to 1, will give the Peak/R.M.S. ratio of the series (2)—that is, the maximum obtainable for a series with these coefficients by altering the relative phase of the components. If, instead of measuring the Peak/R.M.S. ratio of one output only, arrangements are made to have four outputs having the following properties:—

- (1) Any single component has the same amplitude for outputs I, II, III, and IV.
- (2) Any single component having a phase angle θ (relative to an arbitrary standard) in output I has a phase angle of $\left(\theta + \frac{\pi}{2}\right)$ in output II, $(\theta + \pi)$ in output III, and $\left(\theta + \frac{3\pi}{2}\right)$ in output IV.

In the cases in which the Peak/R.M.S. ratio is a minimum for one output,

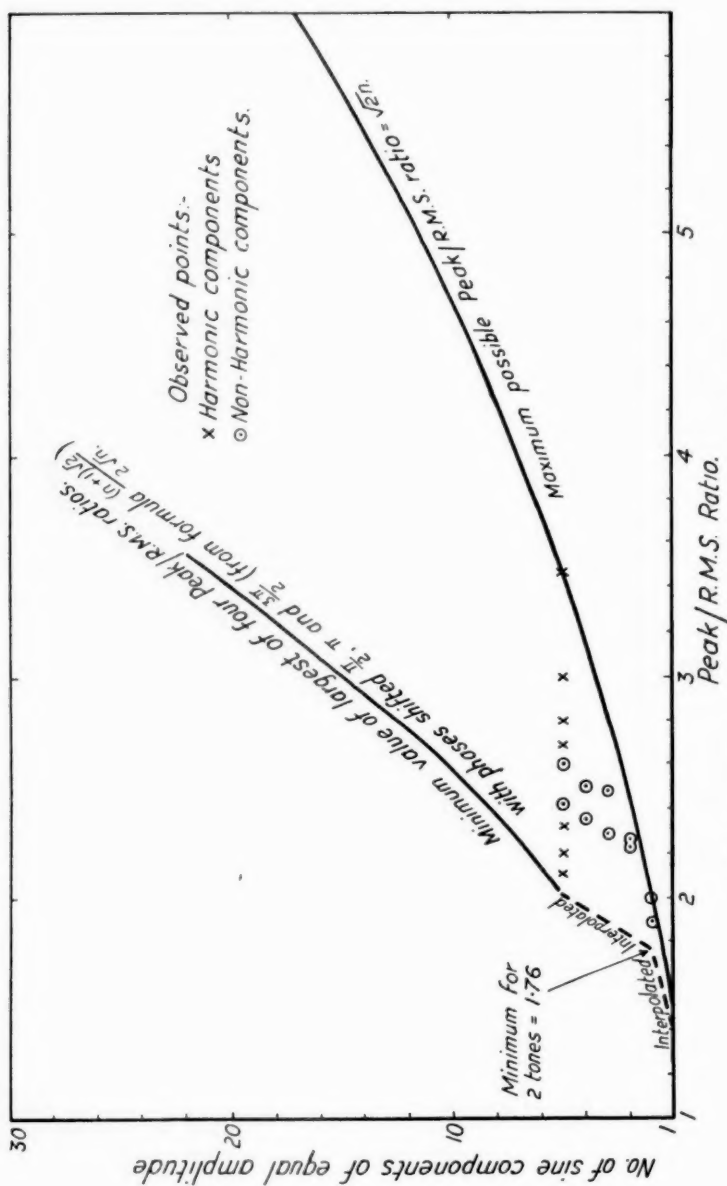


FIG. 3.—Relation between Peak/R.M.S. ratio and number of tones.

it will then be a maximum for one of the others. The Peak/R.M.S. ratios from all outputs are determined and the largest value is chosen, then a series represented by (1) from one output, although it will give a Peak/R.M.S. ratio from that output approaching 1, will give a Peak/R.M.S. ratio from one other output which will be a maximum.

If this method is adopted, it is now only necessary to consider the largest Peak/R.M.S. ratio. This value will vary between certain limits according to the phase relationships of its components as before. The upper limit will still be the same as for a single output; the lower limit, however, will be different.

A number of attempts have been made to determine this lower limit by mathematical analysis, but it has not been possible to find a formula which can be proved mathematically. An empirical formula, however, has been used tentatively, and although it cannot be proved that this formula is correct, no case has yet been found which contravenes it. A large number of cases have been investigated, the actual sine waves in various phase relationships have been drawn out and the Peak/R.M.S. ratios determined graphically.

The following formulae have been adopted:—

If n = the number of tones (all of equal equivalent intensity), the maximum Peak/R.M.S. ratio is

$$r_{\max} = \sqrt{2n};$$

the minimum ratio of the largest of the four Peak/R.M.S. ratios after altering the relative phases as above is taken to be

$$r_{\min} = \frac{(n+1)\sqrt{2}}{2\sqrt{n}}.$$

Fig. 3 shows these relationships graphically; the observed values of diverse electrical combinations of sine waves are also shown in fig. 3. It will be noted that with the exception of some harmonic combinations they all fall within the limits prescribed. The reason why some harmonic tones fell below the limit was found to be due to the fact that the phase-changing circuit in these experiments was not sufficiently accurate and did not give the required outputs with the phase shift, as specified. This defect was remedied in the subsequent experiments. For two tones it is possible to determine r_{\min} by calculation. It is found to be 1.76, which is larger than the minimum given by the formula (1.5). In figs. 3 and 4 this has been taken into account when drawing the curves.

Fig. 4 shows the limits of the correction for various maximum Peak/R.M.S. ratios, based on the results shown in figs. 1 and 2. If a correction

is applied on the basis of the curve designated "Mean Correction" in fig. 4, the results will in all cases be within ± 5 db. In most cases the results

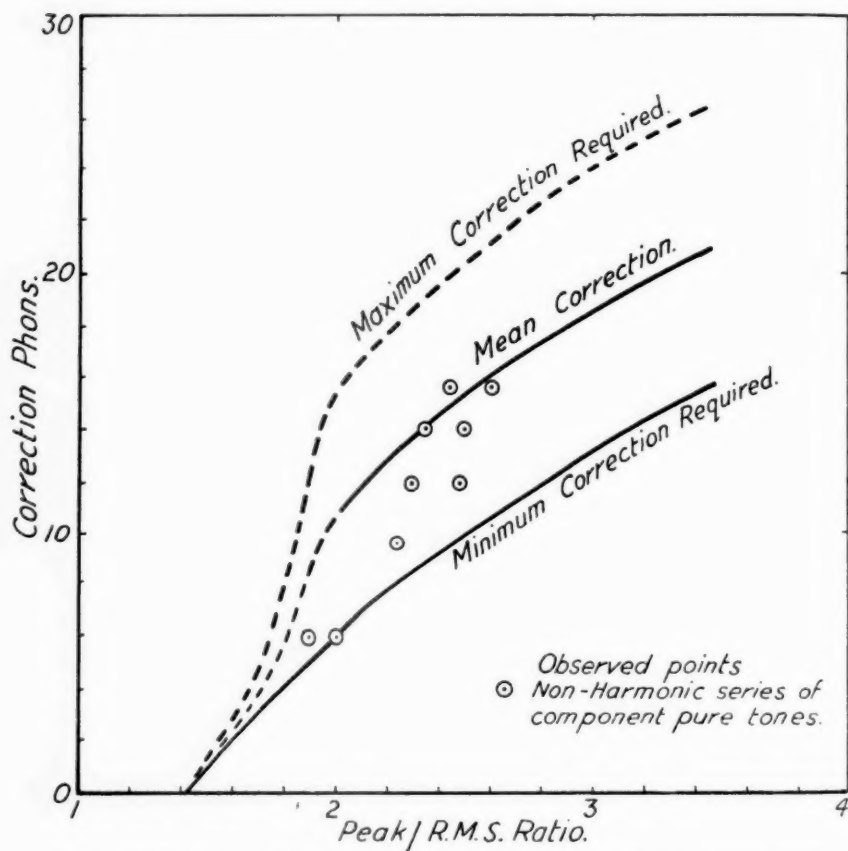


FIG. 4.—Relation between Peak/R.M.S. ratio and correction required at an equivalent energy reading of 40 phons.

will be more accurate, because the maximum and minimum relations only occur when harmonic components having definite phase relationships are measured. Fig. 5 shows the mean correction for different equivalent energy levels.

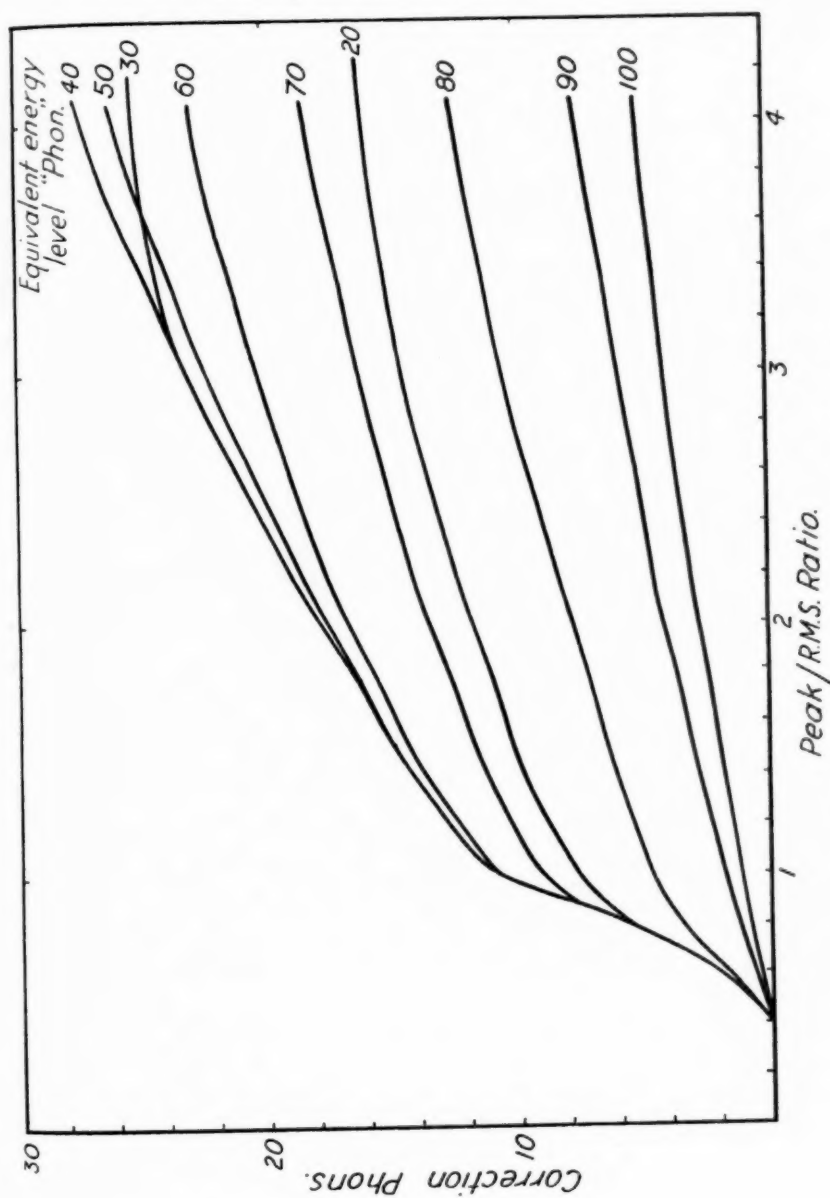


FIG. 5.—Correction curves for objective noise meter at different levels.

V. PRACTICAL CONSTRUCTION OF AN INSTRUMENT USING THE PEAK/R.M.S. RATIO TO CORRECT FOR COMPOSITE TONES.

To construct an objective noise meter using the Peak/R.M.S. ratio to determine the correction required for composite tones, a circuit on the lines shown in fig. 6 is necessary.

The noise to be measured is picked up by the microphone and the resulting potential is amplified, passed through the weighting network to obtain correct pure tone response, and then passed on to the special circuit giving four outputs, each with a phase difference of 90° . From the R.M.S. outputs (which should all be equal) the "equivalent energy" is determined, *i.e.* the equivalent loudness which would be correct if the noise consisted of a pure tone. In practice it is not possible to make all the R.M.S. outputs equal for tones of all frequencies, but by means of the circuit described subsequently they can be made to read within 1 db. This is sufficiently accurate for the "equivalent energy" determinations but not for the determination of the Peak/R.M.S. ratios. The Peak/R.M.S. ratios of each output are then determined, and from the largest Peak/R.M.S. ratio and the "equivalent energy" the correction to be added to the "equivalent energy" is obtained from fig. 5.

The circuit for giving the four outputs with 90° phase shift between each is given in fig. 7. It will be realised that the difficulty is to obtain a circuit which gives two outputs differing by 90° in phase but equal in intensity at all frequencies. It is in fact impossible to construct a circuit which will do this accurately, but the one given in fig. 7 has a performance which is sufficient for practical purposes. The phase differences between outputs I and II are given in fig. 8 as a function of the frequency. Outputs III and IV, being 180° out of phase with outputs I and II, are obtained by the use of a centre-tapped transformer. The R.M.S. value of outputs I and III are equal as well as the R.M.S. value of outputs II and IV. The arrangement shown in fig. 6 for measuring the R.M.S. and the peak consists of a combination of electrostatic voltmeters and rectifiers. The electrostatic voltmeters directly across the transformers measure the R.M.S. outputs I and III and II and IV (because $I = III$ and $II = IV$ two only are required). The rectifiers and electrostatic voltmeters which follow are arranged so that they automatically choose the maximum peak from each pair.

Four readings are taken. The two readings on the R.M.S. meters (which are always within 1 db. of each other) indicate, firstly, the equivalent energy or uncorrected objective noise meter reading. Secondly, they are used in conjunction with the respective peak meter readings to determine the Peak/R.M.S. ratio of each pair of outputs. From the maximum

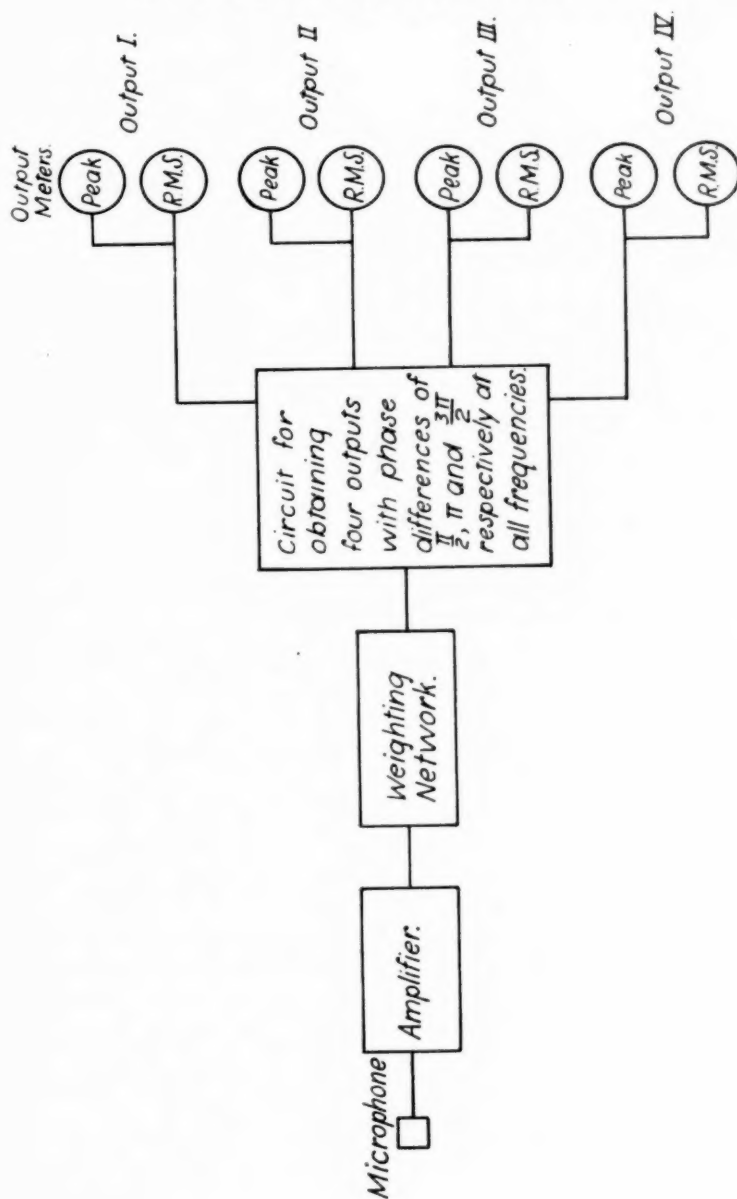


FIG. 6.

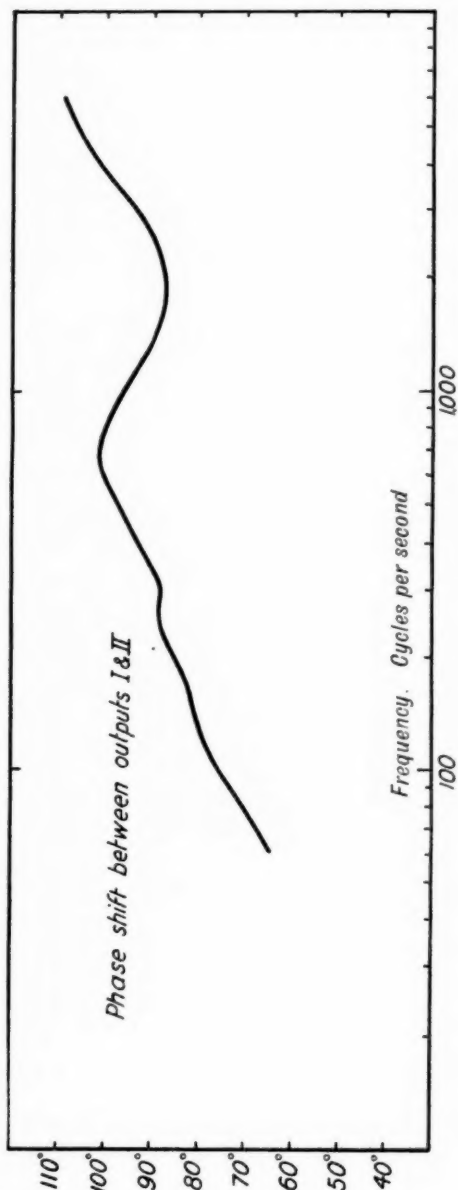


FIG. 8.—Phase-changing device.

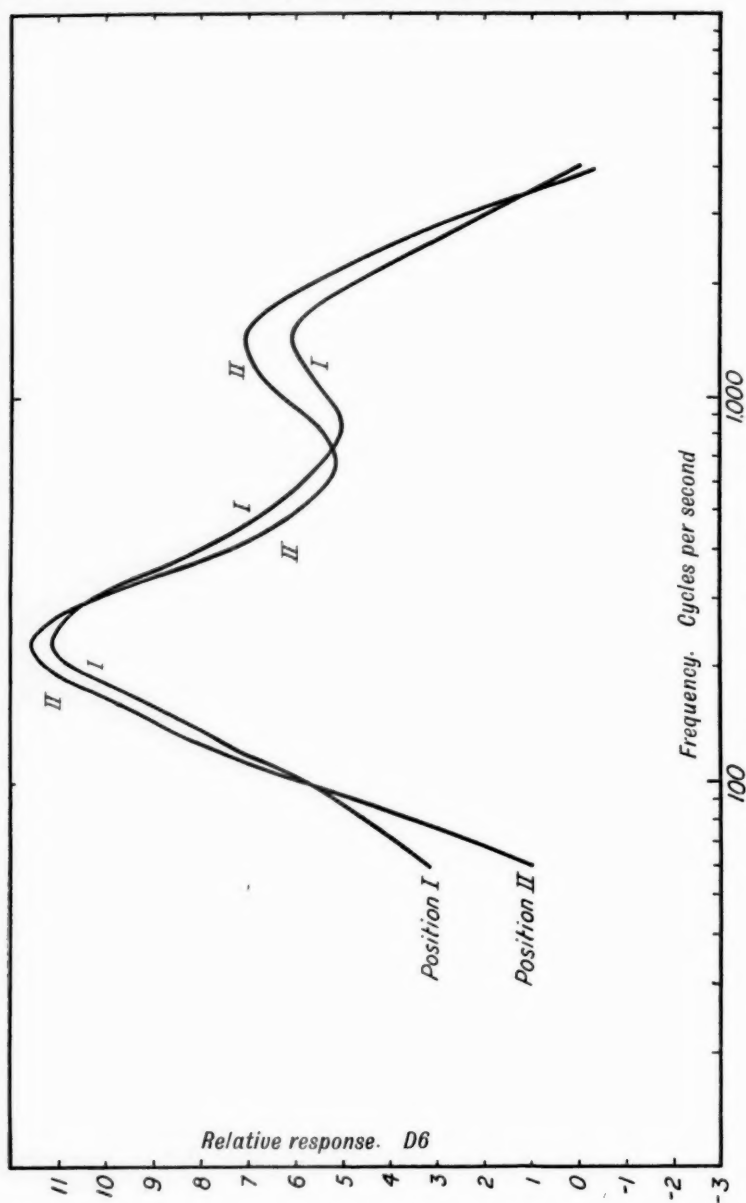


FIG. 9.—Phase-changing device response curve.

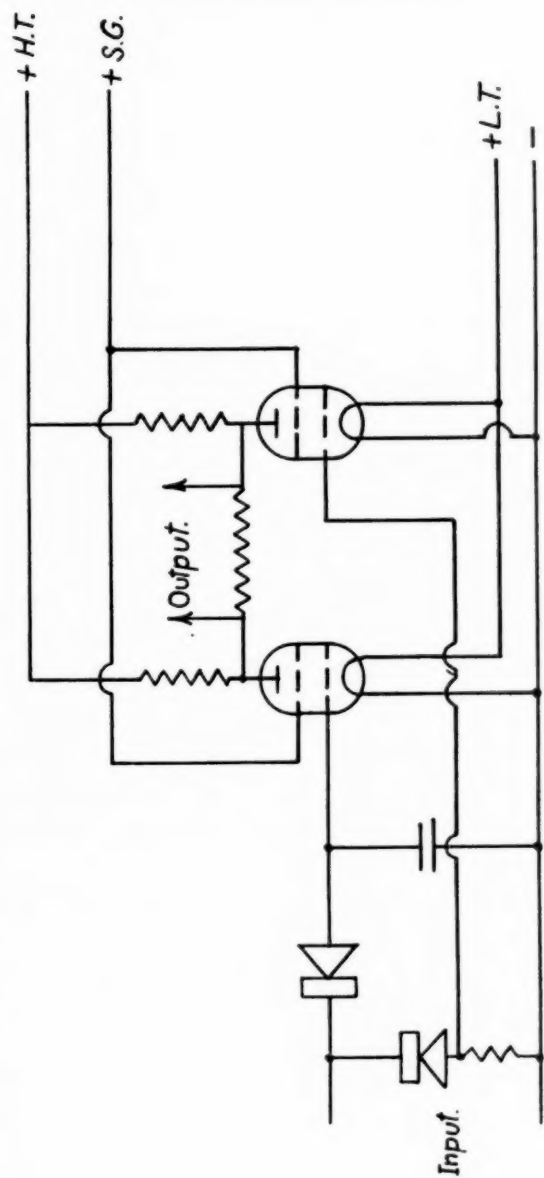


FIG. 10.

Test No.	Type of noise on number of tones.	Equivalent energy (sound level db.).	Maximum Peak R.M.S. ratio.	Correction. Phon.	Corrected equivalent loudness. Phon.	Error.	Equivalent loudness by standard method. Phon.	Equivalent loudness based on maximum peak reading. Phon.	Error.
1	Harmonic noise 6 equally loud tones	37	2.05	12	49	-4	53	40	-13
2	Harmonic noise 6 equally loud tones	67	2.05	10	77	-1	78	70	-8
3	Non-harmonic noise 6 equally loud tones	39	2.39	14	53	+1	52	43	-9
4	Non-harmonic noise 6 equally loud tones	67	2.50	12.5	79.5		79.5	72	-7.5
5	Relaxation oscillation	50	4.05	22	72	-1	73	59	-14

Peak/R.M.S. ratio and the equivalent energy, the correction to be applied to the R.M.S. reading can then be found from the curves given in fig. 5.

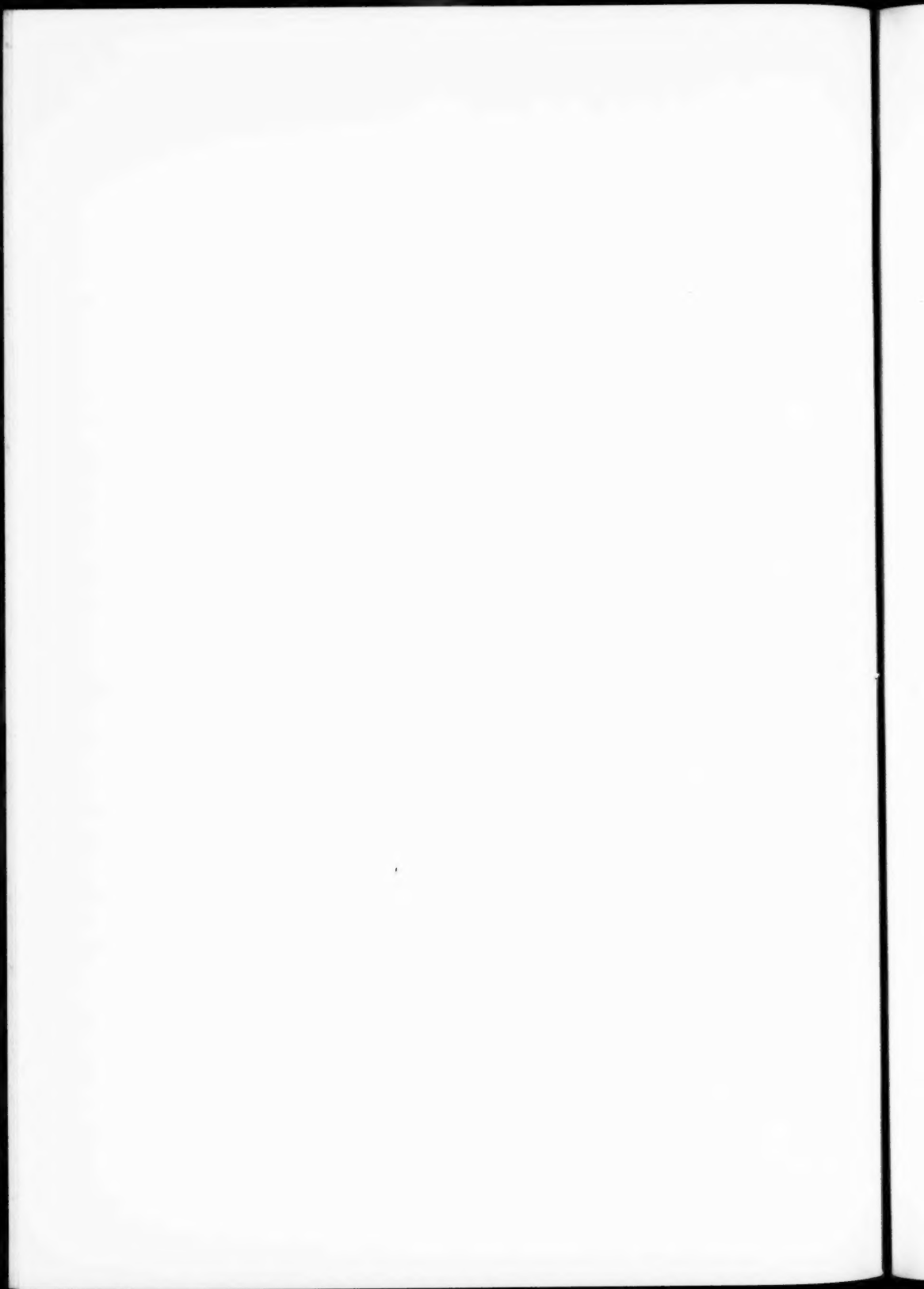
Fig. 9 shows the response curve of the circuit described; it will be noted that between 80 cycles and 4000 cycles the two pairs of outputs are within ± 1 db. of each other.

The table shows some measurements made with an instrument constructed on these lines. It can be seen that for sustained noises the results agree well with those obtained by the standard method. On the other hand, it is seen that a peak reading alone does not give a sufficient correction at medium intensities.

As at present constructed, four readings are necessary to measure the equivalent loudness of a noise, but it would be possible to make the whole instrument automatic. A circuit to give an automatic indication of the Peak/R.M.S. ratio is given in fig. 10. The output from such a circuit could be used to alter scales, bias valves automatically, adjust attenuators, etc., so that a direct indication of loudness by means of an instrument constructed on these lines would be possible.

VI. ACKNOWLEDGMENTS.

The author wishes to thank Mr. B. G. Churcher, under whose direction the work was carried out, and Mr. A. J. King for several valuable suggestions.



A STONE BEAD INDUSTRY OF THE WESTERN TRANSVAAL.

By HAROLD S. HARGER, F.G.S.

(With Plates XLV-XLIX and five Text-figures.)

(Read May 17, 1939.)

INTRODUCTION.

A recent careful investigation of South African and other archaeological literature revealed to the writer that the stone bead is a very scarce variety of artefact, not only in this country but throughout the world. References to beads made from ostrich shell are numerous, and the use of this particular ornament, probably originated by the primitive Bushman, has spread to the Bantu tribes, some of whom are making them in the S.W. Africa Protectorate at the present day. The stone bead of local make, on the other hand, has been very rarely met with until recently, and this fact provides justification for recording the discovery of an old bead industry in the Transvaal.

The serpentine beads, herein to be referred to, were first discovered by the writer and his prospector, C. P. Engelbrecht, during the last few years. The first factory site produced only a few whole beads and cylinders (from which they were cut) and many more broken beads, but last year a second site in the same area yielded a larger and better supply. From the entire collection we are able to ascertain the process of manufacture from beginning to end. The collection has been presented to the Harger Archaeological Collection, which is housed in the Public Library, Johannesburg, and can there be examined by interested persons.

The first find was made on Nooitgedacht, No. 405, less than 5 miles north of Zwarttruggens in the Rustenburg District, Transvaal.

The second was made last year on Winkelhaak, No. 280, by C. P. Engelbrecht, at a point about $2\frac{1}{2}$ miles east of the first.

Recently another find of serpentine beads was brought to my notice by Mr. Engelbrecht. This discovery was made on the farm Magoza Stad, No. 279, about 11 miles east of Zeerust. Ten of the beads in a smoothed and finished state, ready for a necklace, were picked up by a son of the owner, Mr. G. C. L. Rootman, who was good enough to hand them to the writer for the Harger Collection.

OTHER STONE BEAD DISCOVERIES.

Very few references can be found relating to stone beads in the archaeological literature of South Africa or elsewhere. Peringuey illustrates two beads in his well-known work, "The Stone Ages of South Africa" (1). One (Cut 3) measures $\frac{5}{16}$ in. by $\frac{5}{16}$ in., and the other (Cut 2) $1\frac{1}{4}$ in. by $1\frac{1}{4}$ in. They are both rounded and smoothed and drilled from pole to pole like the "Kwi" or digging-stick weight. Peringuey terms them "unique" examples, but does not state of what rock or mineral they were made. They were found beneath several feet of bat guano in a cave at Montagu, C.P., in the company of a wooden club of phallic design, and are probably not extremely ancient.

A stone bead, $\frac{1}{2}$ in. diameter, found in Khama's country by Dr. S. Schonland, was picked up on the site of an "Ancient Mamangwato Settlement" (2). It was found 43 miles north of Serowe, and had a "double bell-mouthed perforation" like the "digging stones." Chief Khama informed Dr. Schonland that "his people used to make such beads." From all the facts given one may judge that this bead was probably of Bantu make, as suggested by the author of the paper.

Some other rather uncommon stone beads found in South Africa, which have been recorded, are those described by W. A. Anderson (3). These were cylindrical, up to 1 in. long, and of hexagonal and octagonal shapes. The holes were perfectly cylindrical and bored parallel to the longer axis. The beads were of agates, carnelian and jasperoid rocks, ground and polished. A "large number" of these beads had been picked up at different times by the natives in the neighbourhood of Inhlanhlimhlu Hill, on the coast of Alfred County, Natal. The beads were fractured and rounded by attrition. The legend relating thereto states that they were only found after a ship ("a great white form") had passed that way (probably before the advent of the white man), and might consequently have been imported from overseas.

An extremely interesting discovery of stone, glass, and ivory beads in a Kalahari cave was made a few years ago by Mr. P. Von Dornik Plater of Johannesburg, a brief account of which appeared in a local newspaper (4). I had the privilege of being shown these beads by Mr. Plater. All except two are ancient glass beads of various shapes and sizes and eight shades of colour. The smallest are coloured trade beads irregularly made, and possibly of early Venetian manufacture; the largest are dark yellow balls $\frac{3}{4}$ in. diameter. Amongst them are crudely made cylindrical shapes $\frac{1}{2}$ in. long, of various shades of green, yellow, etc., and ivory beads shaped like the finished Magoza Stad examples in text-fig. 2. Of equally great interest is a beautifully finished bead of cream-coloured marble, a sym-

metrical, slender, barrel-shaped bead, $1\frac{3}{8}$ in. long by 1 in. wide across the centre. It has been bored in a most remarkable manner, the hole being longitudinally drilled to a diameter of only 1.5 mm. Such a small hole for a stone bead of its size and weight is extraordinary, and the necessity for a hole so diminutive is difficult to account for. Quite the reverse is the second stone bead of dark greenish serpentine, spherical in shape, 1 in. wide by $\frac{3}{4}$ in. deep, the hole in which is $\frac{3}{8}$ in. diameter at one end and $\frac{5}{16}$ in. at the other. The marble bead closely resembles Peringuey's "unique" example shown in his Cut 2—fig. 188, pl. xxv—previously referred to (1).

Charles Darwin (5) also refers to stones of various colours with cylindrical holes which were found in vast numbers by the Indians on a certain hill in the Argentine, and used for the purpose of making necklaces and bracelets. The place was named Sierra de las Cuentas, which signifies "the hill of beads," and the name suggests that there had been a stone bead industry of some importance there.

Stones supposed to have been perforated "naturally," and perhaps used as beads, also some square beads of steatite, are recorded by Alanson Skinner (6) in a memoir on the Indians of Manhattan Island, U.S.A. The method of perforation in the last case appears to be somewhat mysterious, as geologists know of no "natural" method of piercing small stones suitable for beads.

Some stone beads from the cave of Mirabel (Drome) in France were exhibited in the British Museum some years ago, but I omitted to obtain information regarding the nature of the rock from which they were fashioned. They formed part of a large collection presented by M. Leon Morel of Rheims (7).

Evans mentions beads formed of quartz pebbles and "neatly pierced pebbles of rose quartz" found in France, also some flat beads of shale from Northumberland (8).

Some beads of callais, "a mineral not known to occur in Europe," are recorded briefly by Lubbock (9) as having been found in the tumuli of Brittany and some other parts of France. Callais is another name for turquoise, and was termed *calaite* in ancient times.

An important discovery of ivory beads attributed to Aurignacian culture was recently made by Dr. Karl Absalon (10) in Moravia, accompanied by some plastic figurines of steatopygous women with strong affinities to the primitive bushwoman of South Africa. They were made by reducing mammoth ivory to suitable rods, which were afterwards rounded and cut into thick discs and cylinders of the garden-roller type, closely resembling some of the Zwartruggens beads (Pl. XLVII) but with wider holes.

About 200 Cro-Magnon beads of ivory are described by Dorothy Davison (11), who also illustrates the manner in which the ivory rods were sawn and gradually reduced to roundish beads. The procedure is precisely what the writer has envisaged as the method adopted at Zwartuggens, with the difference that whereas Cro-Magnon man used flint saws and produced a V-shaped cut, the Zwartuggens worker used iron or steel and produced a cut with parallel sides.

Reference to beads made from marine shells, ostrich egg shells, ivory, bone, amber, jet, baked clay, and other soft substances, also of glass and porcelain (trade beads), are frequently met with, but records relating to the fashioning and drilling of beads from stone of any sort are comparatively rare. This fact makes the discovery of a stone bead industry in the Transvaal all the more interesting.

TOPOGRAPHY AND GENERAL FEATURES.

The farms on which the beads were made are situated in the rugged country between Zwartuggens and Zeerust, which has been drained and deeply sculptured by the Elands and Marico Rivers, and their numerous tributaries in the Western Transvaal. The severe and long-sustained erosion of the past has left hill ranges and kopjes standing to heights approaching 700 ft. above the surrounding normal levels. The altitude is between 3500 and 4000 ft.

The geological formation on Nooitgedacht and Winkelhaak consists almost entirely of basic amygdaloidal lavas of the Transvaal System, and the weathering of these rocks has produced innumerable roundish boulders. These lay ready at hand on the surface, and were of great convenience and use in the building up of kraal walls for herding live stock and protecting them from the carnivora that abounded in early Bantu times.

The formation on Magoza Stad is mainly andalusite slates of the Daspoort horizon (Transvaal System) and contemporaneous lavas, and later intrusive diabases.

On Nooitgedacht the writer, when making a geological survey, observed a serpentine dyke of post-Daspoort age before any beads had been found. Its fresh and easily cleaved outcrop was probably the prime factor in the establishment of a bead industry in the vicinity. This dyke is situated roughly midway between the two bead factories on Nooitgedacht and Winkelhaak, which adjoin each other. There is probably a serpentine dyke on Magoza Stad also, although not yet located, as two small blocks of serpentine were picked up on that farm near the old ruins of a native village.

The area we are dealing with is well watered throughout by several perennial streams and many springs. Indigenous trees and bushes suitable for fuel are plentiful everywhere; the pasturage is good, and the valleys

contain rich dark loam well suited to the cultivation of native cereals and other vegetable foods and fruits. For these reasons this picturesque and fertile land was excellently adapted to the needs of the Bantu peoples who occupied it in large numbers for centuries. In the early part of last century the Zulu hordes of Moselekatse laid the land waste by slaughtering the people, destroying their villages and raiding and capturing their live stock. To-day the sites of these villages are recognisable by the tumbled kraal walls and heaps of stones removed to clean up the dwelling sites, but not a single fragment can be found of the once numerous huts that housed a prosperous and happy people. Sub-aerial denudation has removed all vestiges of the wattle and daub structures that had formed the homes of thousands of Bantu people in this warm and once thickly populated area. Accumulated boulders of diabase and remnants of stone cattle kraals alone are left to tell of the past; and it is amongst the ruins of these villages that some serpentine beads, and fragments of the serpentine rock from which they were made, are to be found if carefully searched for.

Long before the advent of the Bantu peoples primitive man in considerable numbers had been attracted to this region in search of the amenities of life called for by exigencies of the period. A warm climate, water, and game in abundance were his principal needs. Stone implements often deeply weathered and patinated and covering many of the stone cultures from Stellenbosch (Chellean-Acheulean) to Smithfield (Aurignacian-Magdalenian) were lying in and on the surface soil long before the arrival of the Bantu. A wide range of stone implements can easily be collected, including *coups-de-poing* and axes of Stellenbosch types, points, knives, scrapers, borers, chopping tools, cores, and playing balls of the later Bushman. These are strewn about profusely (especially on Magoza Stad), and consist of various rocks and minerals such as diabase, quartzite, slate, indurated shale, chert, flint, quartz, agate, and chalcedony. Their state of preservation and sometimes the depth at which they are found indicate strongly that they greatly exceed in age the serpentine beads found in the same region.

THE FACTORY SITES.

The most interesting and productive factory site is on Winkelhaak, about 1200 yards from the Elands River on the east bank. This portion of the farm is owned by one Blanche, and contains a small spruit which flows westerly into the Elands River. Up the south bank of this spruit are some clearings amongst the bushes and rocks where native kraals had at one time existed; and in these cleared spaces a good and complete range of the serpentine artefacts was found. On two of these cleared spaces numerous fragments of serpentine lie about. They rarely reach 2 in.

across, and are all very angular and fresh. Many of the pieces are easily detected, as their light bluish-grey colour is in strong contrast to the rich red soil produced by the weathering of the underlying basic rocks. The cylinders and beads, however, are often discoloured by the clayey soil in which they have been lying.

The uppermost site produced the largest number of cylinders, beads, and chippings; also a slate pendant (Pl. XLVII, No. 1) and two small pear-shaped gold beads. The second site, about 80 yards lower down the slope, produced, in addition to cylinders and beads, a thin oblong pendant of serpentine with a hole in the middle (text-fig. 1).



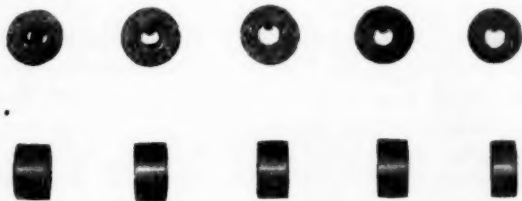
TEXT-FIG. 1.—Serpentine pendant. (Nat. size.)

Several bits of very much corroded iron, which might have been used as boring tools (text-fig. 3), were found in this area. Another uncommon artefact found here was a block of shale measuring $17\frac{1}{2}$ in. by 5 in. by 2 in. thick containing a curved groove 1 in. wide by $\frac{3}{16}$ in. deep, which might have been used for smoothing the wooden shafts of spears and knobkerries. The groove looks rather too wide to have been a bead smoother (Pl. XLVIII).

The site on Nooitgedacht, where the first beads were found, is situated on the west bank of a stream which passes in front of the residence of the owner, Olivier, on its way easterly to join the Elands River. This site, like the others, doubtless once possessed a number of native habitations, and was conveniently placed just above a fountain which, in bygone days, flowed strongly, but to-day only shows water a little below the surface-level.

Overlooking the fountain and along the bank of the spruit, some serpen-

tine beads and cylinders were picked up by the author on the surface; whilst nearby some small copper beads of native manufacture were found in the washing-machine when the writer was testing some diamond-bearing surface rubble of an eluvial nature. In an older rubble close by, at a depth of 4 ft., some diabase *coups-de-poing* of Chellean types and crude workmanship were unearthed. They were all deeply weathered and decomposed to a reddish earthy substance on the external zones. A number of these old palaeolithic implements were collected. No copper or serpentine beads were observed in this ancient rubble, which was undoubtedly deposited long before the advent of the Bantu people.



TEXT-FIG. 2.—Finished beads. (Nat. size.)

The workshop site on Magoza Stad is on G. C. L. Rootman's portion of the farm, north-west of his homestead. The area is to-day covered with fairly thick bush containing big indigenous trees, some of which are growing within the tumbled walls of kraals which at one time herded live stock. A large native village once occupied this extensive area, which lies between the foot of a long high kopje of andalusite slate and diabase, and the west bank of the Wilgeboom Spruit: a rapidly flowing perennial stream passing through a valley of rich alluvium.

The beads found here (by a son of the owner) were of serpentine and copper, the former being all in a perfectly finished state (text-fig. 2). They might have belonged to a single necklace. The writer did not see unmistakable signs of the actual factory site in this bush-clad area, but two squarish, sawn blocks of serpentine, and a few short cylinders and a sawn-off disc indicated its proximity. It is likewise possible that there is a serpentine dyke on this farm (as on Nooitgedacht), but it has not yet been discovered or looked for.

At the old village, close to where the beads were found, one can find fragments of furnace slag scattered about the surface, some bits of tuyères, and also the partly denuded foundations of the old furnaces. Iron ore of

the specular hæmatite variety was used, and pieces of the ore still lie around the furnace site. The source of the ore is near at hand on the hill overlooking the factory site, and also on Dammensburg (adjoining on the north-west), where extensive native workings are exposed in a hill face. The ruins of a large native smelting furnace can still be seen at the latter place according to a local farmer, Mr. F. C. Van der Linde of Goedgeleeven, No. 285.

A native-made soft iron hammer was also found on Magoza Stad. The ends were much rounded by wear and very badly burred over. Its weight is about $3\frac{1}{2}$ lbs. The hole for the handle was larger at each end than in the centre, where it was about $\frac{5}{8}$ in. diameter. Only a solid iron handle could have been used to withstand any sort of blow with a head of the above weight. A wooden handle would have been quite useless, especially as the hammer had probably been used for spalling blocks of iron ore intended for the furnace.

Small pieces of pottery belonging to broken pitchers are fairly plentiful about these old native ruins. Some of the pieces have impressed patterns, as is common with Bantu work, but as such designs have extended over a considerable period of time it is doubtful if they can be depended on to reflect the age of the serpentine beads. A number of the impressed fragments were, however, collected for the purposes of research, and will form part of the collection relating to the present subject.

From the foregoing particulars it will be gathered that the serpentine bead factories were all associated with native habitations which time and the elements have completely obliterated. Only the tumbled cattle kraal walls, consisting of resistant diabase boulders, remain as pointers to the sites of such villages.

The presence of old furnace slags, a clumsily made iron hammer, ornamental stone pendants, gold beads, a steatite mould, pottery, and other things combine to indicate that the serpentine bead industry was established by an early Bantu tribe in pre-European times.

THE BEAD INDUSTRY.

The beads are made of serpentine, the hardness being 3 in Moh's Scale. The fragments of serpentine rock found on the factory sites have, doubtless, been obtained from the outcrop of the serpentine dyke on Nooitgedacht found by the author. The pieces required for bead-making could easily be carried to the work sites situated less than 2 miles distant in each case. On Magoza Stad two blocks of serpentine were found, and each of them had been sawn from a larger block by a metal saw, the cuts being perfectly flat. One piece had two sawn faces, the other had three.

The following were collected at the several sites, the majority from Winkelhaak:—

Cylinders, roughly rounded (Pl. XLV); some short segments of the garden-roller type, ready for boring (Pl. XLVI)	108
Beads, rough and unfinished, but bored (Pls. XLVI and XLVII)	28
Beads, finished, smoothed, rounded, and drilled ready for use (text-fig. 2)	15
Beads, broken, smoothed, rounded, and drilled (Pl. XLVII, bottom)	80
Beads of copper	15
Beads of gold	2

Cylinders.—These vary in length from $2\frac{1}{8}$ to $\frac{1}{2}$ in. (Pl. XLV). The short segments have been cut from longer cylinders. In some cases the cut might have passed right through, but some examples show that the short segments had been broken off after a shallow cut all round had first been made (Pl. XLV, bottom row). The cuts have parallel walls, indicating that a thin metal saw, or thin hard plate with serrated edge, had been used. The cuts could not have been made with stone saws such as were used by primitive man, for the simple reason that the latter would produce a V-shaped cut. These measured are 0.5 mm. and 1.0 mm. in width. On Magoza Stad thin, much-eaten blades of metal, which might once have been saws, were found.

Beads.—The large majority are short cylinders of the garden-roller type bored lengthwise, and resemble in size and shape some of the glass beads discovered (and probably smelted) at Mapunbugwe. Some of the finished beads, as in text-fig. 2, are more discoidal, as if ground down at the ends to produce a flatter bead. The holes are from $\frac{1}{16}$ to $\frac{1}{8}$ in. diameter, truly drilled, and the same diameter at each end. Only one long bead was found, and this was broken after it had been drilled. It was 1 in. long by $\frac{1}{2}$ in. wide. The hole had been truly drilled almost the full length when the bead broke. In very few of the beads had boring been started at each pole. In a few of the examples, especially in the longer segments, the bead had broken before the hole was completed. This could have happened if an iron or steel drill had been operated by hand, in which case a slight swaying from the vertical under pressure would cause the bead to split, as in Pl. XLVII, bottom rows. Some much-corroded pieces of iron were picked up on the factory site on Winkelhaak which, when fresh and in use, might have been thin enough to perform the boring. One of these has been bent to take the palm of the hand and facilitate vertical pressure on the bead (text-fig. 3).

An iron drill-bit, set in a wooden haft about 20 in. long, was used by the women of the Naron tribe in British Bechuanaland Protectorate for drilling ostrich egg shell beads (12). A similar method might have been adopted in the case under review.

Copper Beads.—At each of the factory sites some copper beads were



TEXT-FIG. 3.—Old iron rods, possibly boring tools. (Nat. size.)

obtained. There were 15 in all. They measure approximately $\frac{1}{4}$ in. diameter and $\frac{3}{16}$ in. deep. They are very much corroded, and were found in and on the surface soil with the serpentine beads. They have been made by bending thin strips of copper around a rod about 3 mm. thick, and closing the ends by pressure or blows.

Pendants.—The slate pendant at the bottom of Pl. XLVII, No. 1, was found on Winkelhaak about 80 yards from the serpentine pendant (text-fig. 1). Both contain holes for suspension, and in the latter specimen the hole is as perfectly round as if made by a modern twist drill fixed in an ordinary drilling-machine.

Gold Beads.—Two small gold beads were picked up at the factory site on Winkelhaak whilst searching for serpentine beads. They were different in shape to the latter, being pear-shaped drops with holes bored through

the small end. They have, unfortunately, been lost or mislaid by the finders, Mr. and Mrs. C. P. Engelbrecht.

In view of the discovery of many Bantu gold ornaments at Mapungubwe, in the Northern Transvaal, and many other places, the presence of gold beads in association with our serpentine beads, pendants, and other artefacts is significant, and points strongly to the whole being of Bantu manufacture.

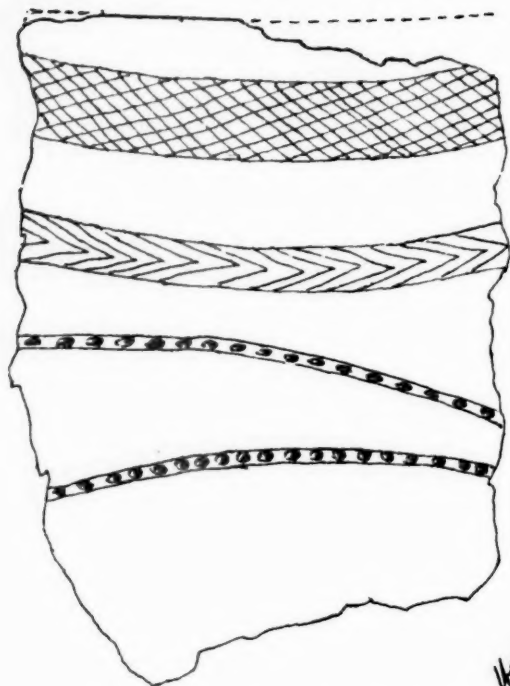
From what has been stated it would appear that the procedure adopted in the transformation of rough fragments of serpentine into beads was as follows:—

- (1) To trim the rough serpentine into longish cylindrical shapes, and round them roughly by grinding.
- (2) To divide the cylinder into sections by sawing deeply enough all round to allow of short segments being broken off as in the Cro-Magnon manner illustrated by Dorothy Davison (11).
- (3) To drill these segments lengthwise for the purpose of forming beads.
- (4) To rub the segments all round, after successful boring, to make the bead smooth for the necklace.
- (5) To grind down the ends on a flat stone so that the chipped or over-bored ends of the holes will be obliterated, and to enable the beads when strung to lie flatly against each other.

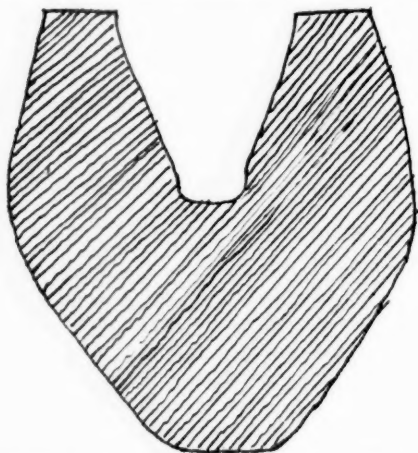
The boring of rough unsmoothed fragments of serpentine (as seen in Pl. XLVII, upper 3 rows) indicates a departure in some cases from the method of sawing segments off cylinders. On account of the breaking of finished or nearly finished beads during drilling operations, after the arduous labour of rounding and smoothing, it would appear that the boring risk was taken sometimes *before* the rounding of suitable fragments. The pieces, moreover, being larger in the rough state were less liable to split when being drilled.

Pottery.—Round about each of the factory sites small bits of native pottery can be observed lying on the surface. Some of them contain impressed patterns. On Winkelhaak, a few feet from the spot where the oblong pendant (text-fig. 1) was found, I observed the upper rim of a clay pot protruding above the surface. It had been buried about 8 or 9 in. in the ground during the erosion and redeposition of the gently sloping surface. It had been broken so that the entire pot could not be unearthed except in loose pieces. A portion of this pitcher is shown in text-fig. 4.

Other pieces of pottery from this and the Magoza Stad sites will be found on Pl. XLIX. Several of these impressed patterns simulate closely, and appear to be related to, some of the Bantu work described and illustrated



TEXT-FIG. 4.—Piece of broken pitcher. (Nat. size.)



TEXT-FIG. 5.—Steatite mould, cross-section. (Nat. size.)

by Laidler in his valuable monograph on South African Ceramics (13), and also by Dart and Nino del Grande (14).

Steatite Mould.—On Magoza Stad, within the confines of the old village where the beads were made, one end of a steatite mould was picked up. It measures $3\frac{1}{2}$ in. long by $2\frac{1}{2}$ in. deep, and is portion of a mould which might originally have been from 7 to 9 in. in length. The interior of the mould is a rounded V shape, as shown in the accompanying cross-section (text-fig. 5).

It is difficult to suggest a use for such a deep mould unless intended for copper ingots required possibly for barter purposes. It may safely be attributed to Bantu culture.

CONCLUSION.

From what has been related it becomes evident that beads as ornaments have a very ancient origin; can be traced well back into neo-Anthropoc times; that the method of fashioning them in prehistoric Europe spread south to Africa, and has continued down to comparatively recent times in the Transvaal and other parts of the sub-continent.

SUMMARY.

From the foregoing will be gathered:

- (1) That the establishment of a serpentine bead industry on the farms referred to in the foregoing was primarily due to the fact that the stone amenable to the fashioning of beads was available on the spot in the form of a serpentine dyke. But for this fortunate circumstance the beads and pendants might never have been produced.
- (2) That the dull serpentine beads must have been made *before* the native artisans had got into touch with the bright-coloured, pretty glass trade beads of later times, for the simple reason that the stone beads would not have been in demand had the more attractive glass beads been known or obtainable.
- (3) That iron or steel saws and drills were used, the availability of which contributed largely to the establishment of the bead industry.
- (4) That the presence of gold beads, apart from other factors, contributes to the belief of the author that the work should be attributed to early Bantu peoples.
- (5) That the presence of clay pottery accompanying the beads, also the remains of smelting furnaces, slag, and hematite iron ore, point to the occupation of the old village and factory sites by Bantu people.

- (6) That the general features associated with the region, the nature of the ornaments and other artefacts accompanying them, combine to indicate that the serpentine beads were the work of a Bantu race in pre-European times, but not of the Stone Age as usually understood.

REFERENCES.

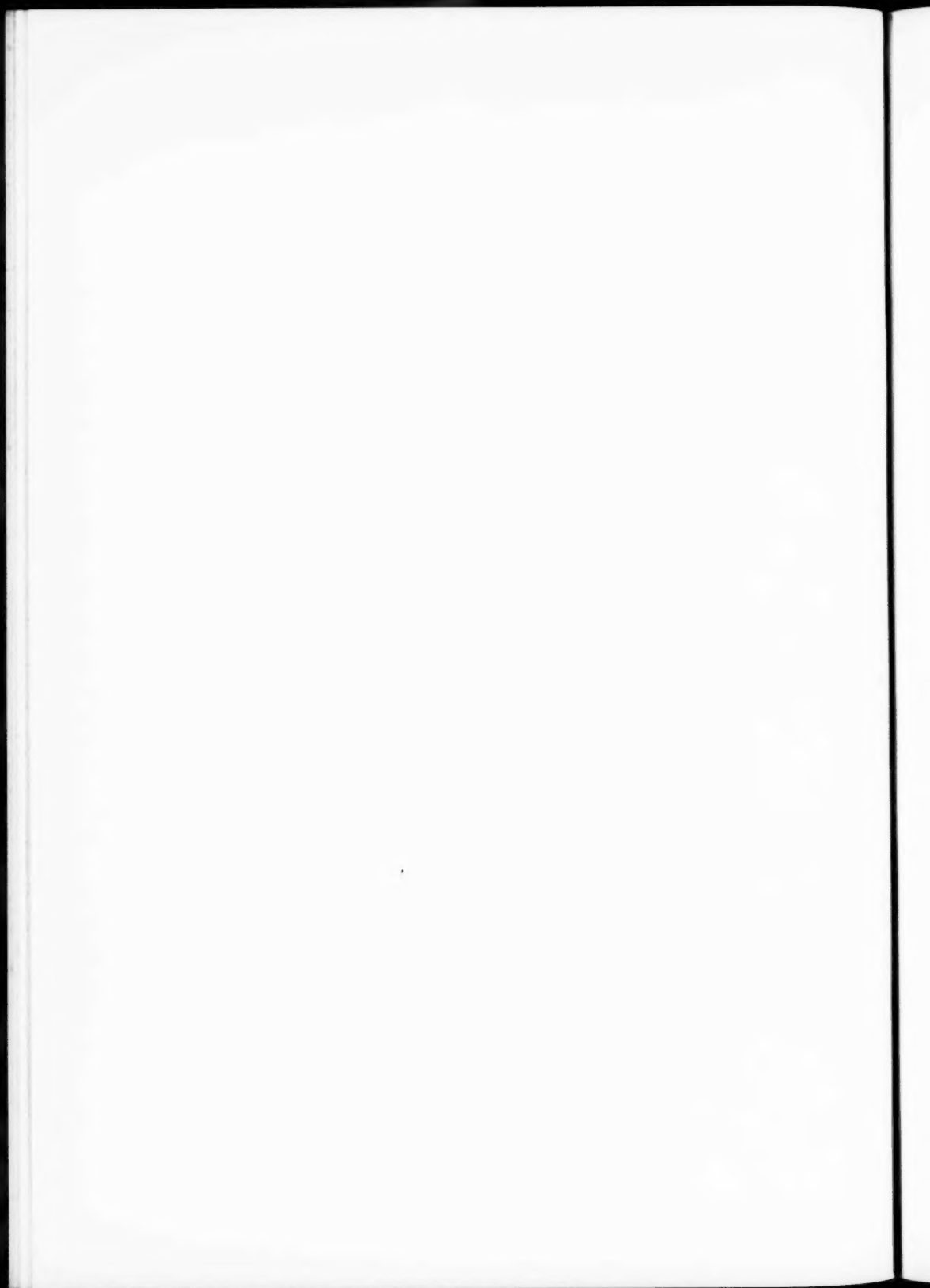
- (1) PERINGUEY, L., "The Stone Ages of South Africa," *Ann. S. Afr. Mus.*, viii, pl. xxv, fig. 188, cuts 2 and 3, and pp. 105 and 165.
- (2) SCHONLAND, S., "On some Stone Implements in the Collection of the Albany Museum," in Report of the S.A.A.A. of Science, 1903, pp. 308 and 309.
- (3) ANDERSON, W. A., Geological Survey of Natal and Zululand, 1907, p. 34.
- (4) *The Star*. Article: "No Room for Relics," 25th September 1936.
- (5) DARWIN, CHARLES, *Journal of Researches*, Ward, Locke & Co., 1910 Edn., chap. 8, p. 155.
- (6) SKINNER, ALANSON, "The Indians of Manhattan Island," *American Museum of Natural History*, Third Edn., 1915, p. 34.
- (7) BRITISH MUSEUM, *Guide to the Antiquities of the Stone Age*, 1921, p. 139.
- (8) EVANS, SIR JOHN, *The Ancient Stone Implements of Great Britain*, 1897, chap. 21, pp. 463-465.
- (9) LUBBOCK, SIR JOHN, *Pre-Historic Times*, 1878, chap. 4, p. 83.
- (10) ABSALON, KARL, "Modernist Moravian Art 30,000 Years Ago," *Illus. London News*, 25th March 1939, pp. 467-469.
- (11) DAVISON, DOROTHY, *Men of the Dawn*, 1934, chap. 13, pp. 100-101.
- (12) GOODWIN, A. J. H., and VAN RIET LOWE, C., "The Stone Age Cultures of South Africa," *Ann. S. Afr. Mus.*, xxvii, 269.
- (13) LAIDLIEB, P. W., "South African Native Ceramics," *Trans. Roy. Soc. S. Afr.*, xxvi (1938), 93-172.
- (14) DART, R. A., and DEL GRANDE, NINO, "Ancient Iron Smelting Cavern at Mumbwa," *Trans. Roy. Soc. S. Afr.*, xix (1931), photo 8, pl. xxxii.



Serpentine cylinders and segments. (All nat. size.)

Harold S. Harger.

Xcill & Co., Ltd.

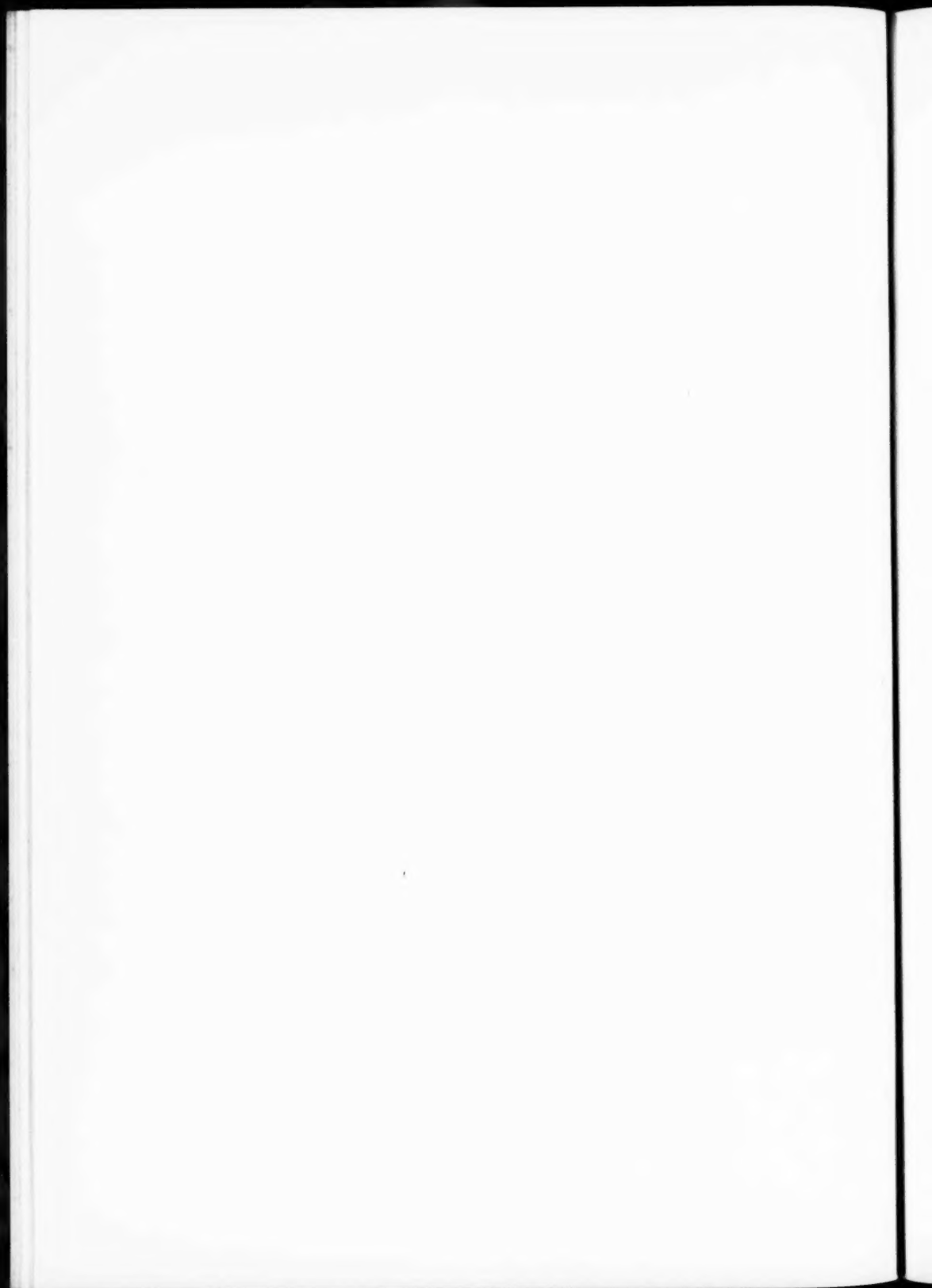


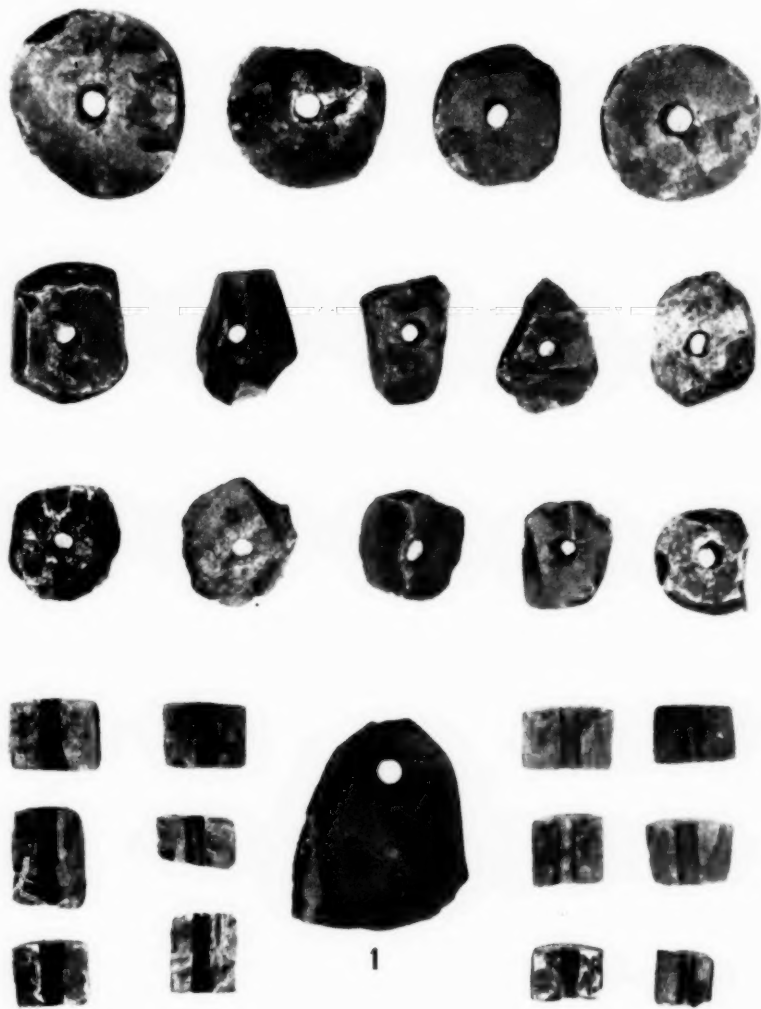


Unbored segments and beads. (All nat. size.)

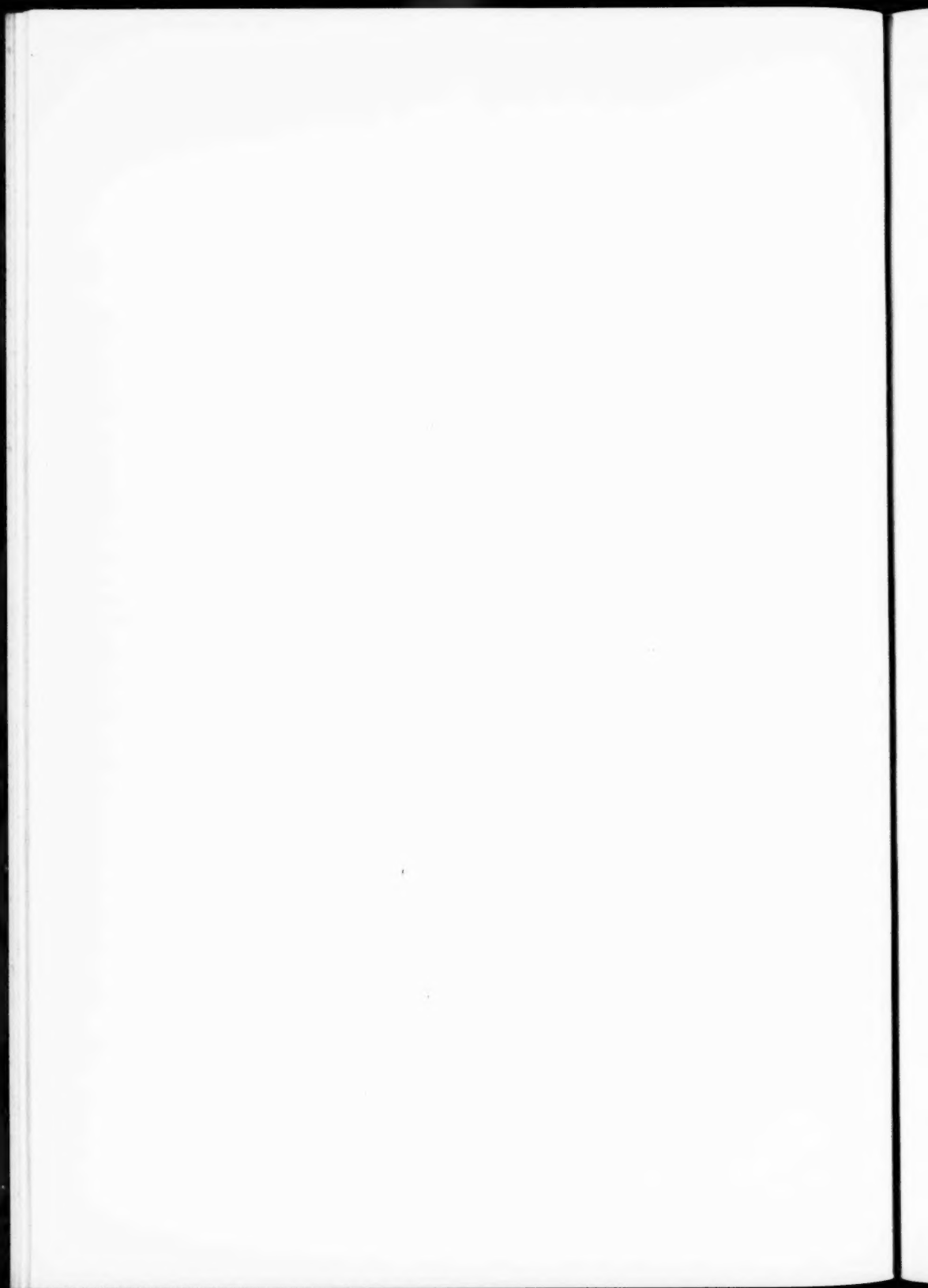
Harold S. Harger.

Neill & Co., Ltd.





Rough pieces of serpentine (bored), broken beads, and (1) slate pendant. (All nat. size.)

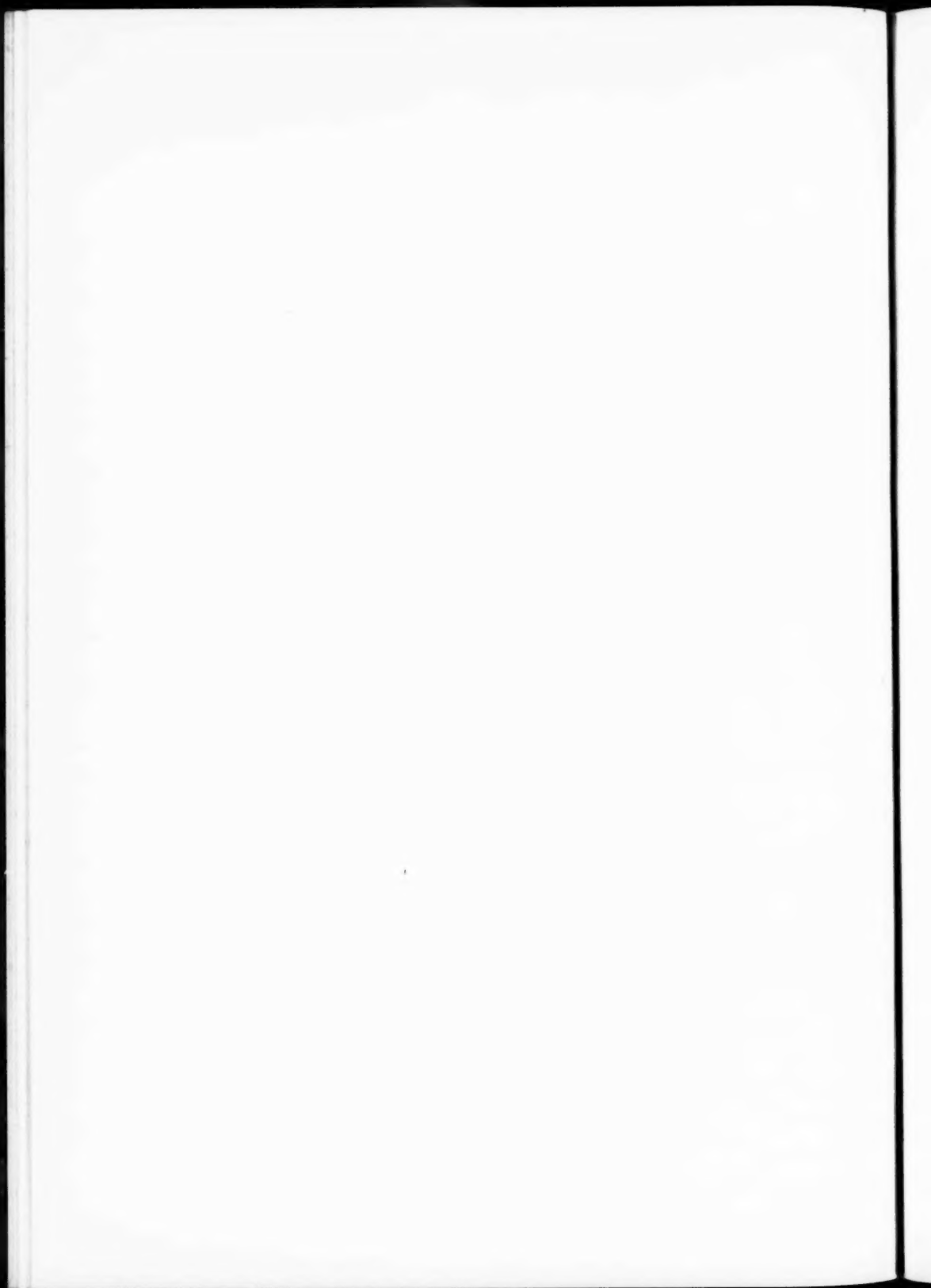


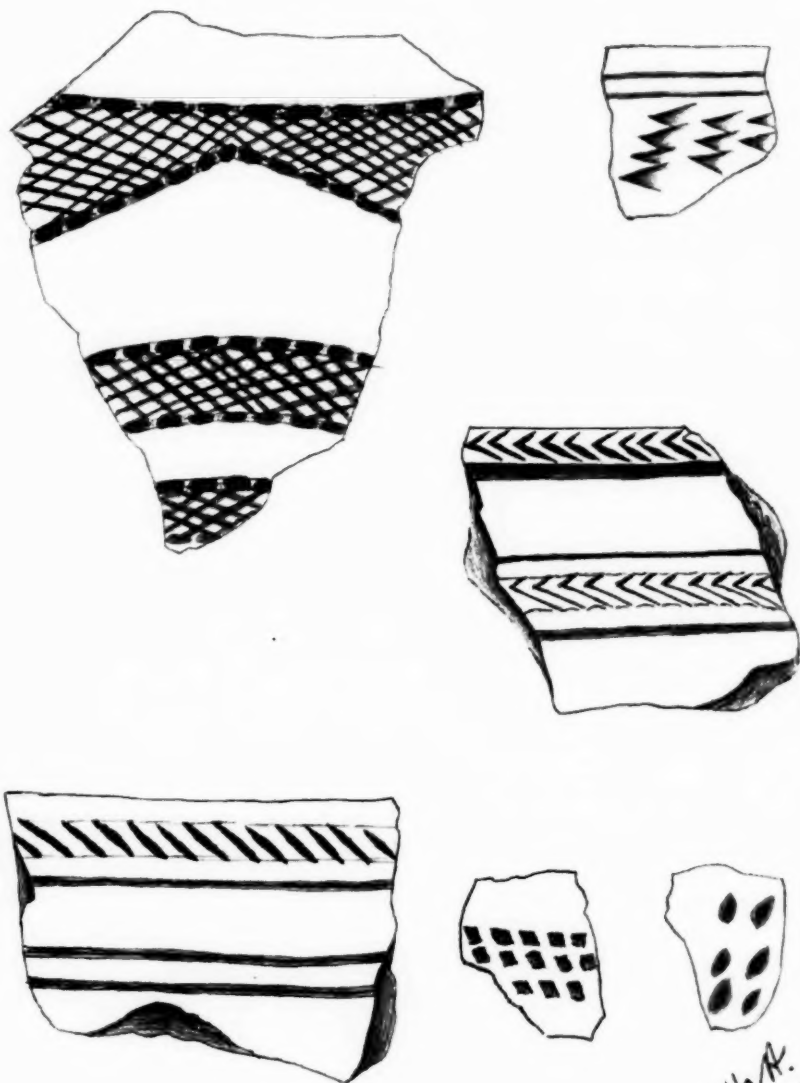


Grooved slab of hard sandy shale, size $17\frac{1}{2}$ in. \times 5 in. \times 2 in.

Harold S. Barger.

Neill & Co., Ltd.



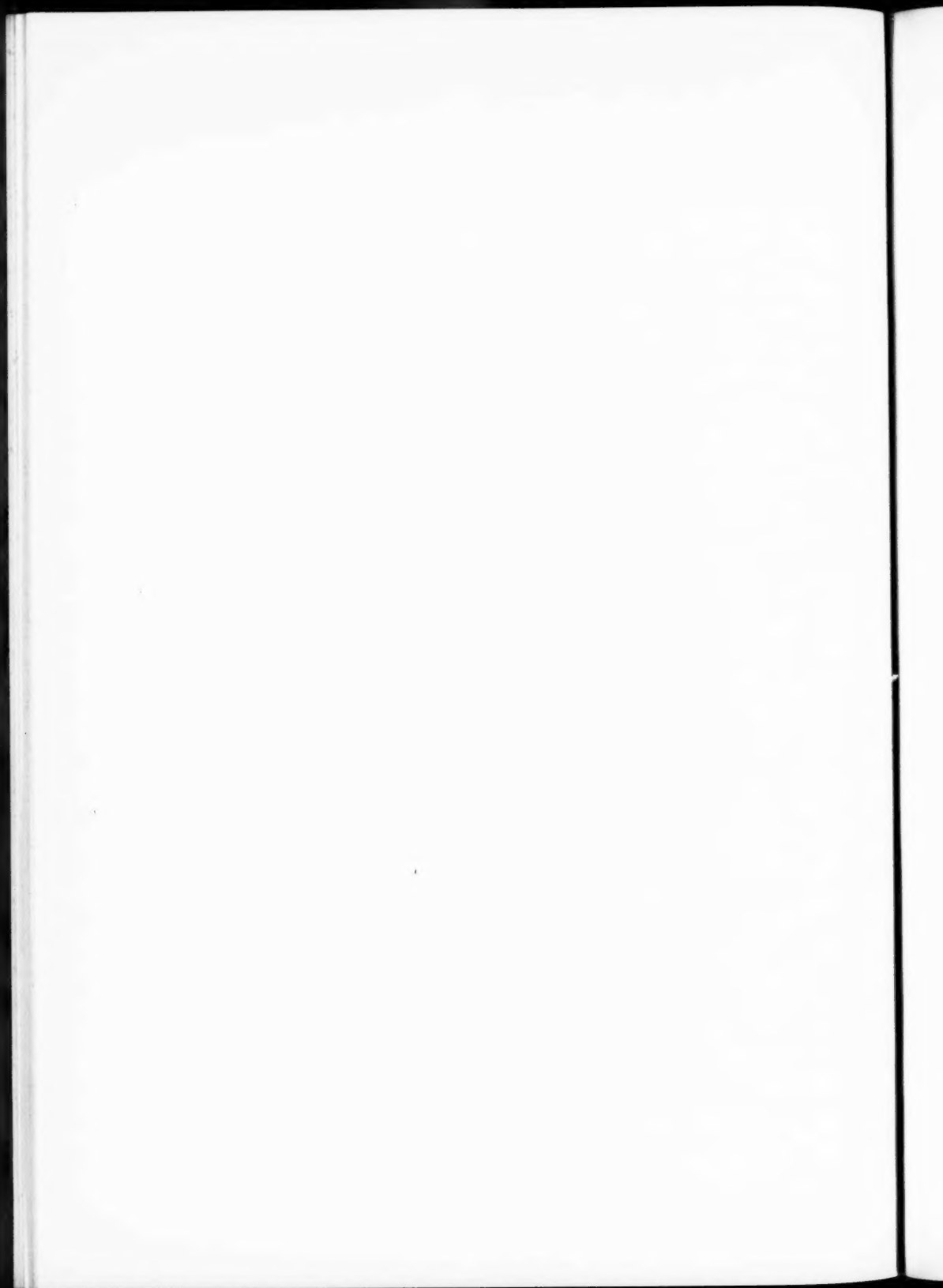


H.A.
4539

Pottery with impressed patterns. (All nat. size.)

Harold S. Barger.

Neill & Co., Ltd.



ELECTRO-MAGNETIC INDUCTION IN WATER.

By H. D. EINHORN, Dr. Ing.

(Communicated by E. NEWBERY.)

(With eight Text-figures.)

(Read August 16, 1939.)

CONTENTS.

	PAGE		PAGE
I. INTRODUCTION	143	(c) Electrode Distance	150
II. METHOD:		(d) Quantitative Relations	151
(1) Arrangement	144	(2) Conductivity	152
(2) Reason for Method	146	(3) Position of Electrodes	152
(3) Magnetic Field	146	(4) Different Electrodes	152
(4) Transformer E.M.Fs. . . .	146	(5) Oscillography	153
(5) Valve Voltmeter and Harmonics	148	IV. PRACTICAL APPLICATIONS	154
(6) Procedure and Computation	149	V. CONCLUSION	155
III. RESULTS:		APPENDIX 1. ON TRANSFORMER E.M.Fs.	155
(1) Induced Voltage and		APPENDIX 2. CALCULATION OF CIRCULATING CURRENTS	156
(a) Flow Speed	150	APPENDIX 3. CORRECTION FOR ERROR INTRODUCED BY DOUBLE-EARTHING	159
(b) Magnetic Field	150		

I. INTRODUCTION.

The electro-magnetic laws as applied to *solid metal* conductors are the fundamentals of electrical engineering, well known and verified in experiment and practice every day since they were stated by Faraday.

How the same laws are to be applied to *fluid non-metallic* conductors has hardly been investigated,* and it is the object of this paper to answer questions such as: What voltage is induced in an electrolyte flowing in a magnetic field? Can we measure this voltage? What are the quantitative relations?

* Experiments on gaseous and solid *non*-conductors moving in a magnetic field have been carried out by R. Blondlot (C.R., 133, 1901, p. 778); H. A. Wilson (Phil. Trans., A, 204, 1905, p. 121); L. Slepian (Ann. d. Phys., 45, p. 861).

It is by no means obvious what to expect. While the opinion * has been voiced that "the free movement of ions may produce voltages higher than in an equivalent width of metal conductor," the opposite † is that "with short poles, the ions, due to their limited mobility, may hardly have had time to move before they are beyond the field, and the p.d. set up would then be very small."

The latter view can be illustrated as follows:—

Suppose water moves in a uniform magnetic field of intensity B (Gauss) at a speed v (cm./sec.), then the induced electric field E (V/cm.) will be $Bv10^{-8}$ and will cause a lateral velocity v' of the ions $= mBv10^{-8}$ cm./sec. where m is the mobility of the ions, which in the case of the H ion may be taken as 3×10^{-3} cm./sec.p.V/cm. ‡ Hence, in a field of 15,000 gauss, $v' = 2 \times 10^{-7}v$, i.e. the angle of drift would be very small and a 5-cm. electrode would receive ions only from a 10^{-5} mm. thick zone close by; but as the flow speed in this boundary layer is unknown (presumably very small) the ultimate effect is doubtful.

On the other hand, calculations carried out by the author (Appendix 2) lead to the result that the electric field set up is independent of the conductivity, hence independent of the mobility of the ions.

An experimental investigation seemed to be worth while for the sake of obtaining a definite answer to the problem.

The only experiments hitherto, as far as the author knows, have been conducted by Faraday § who tried to measure voltages induced in the Thames due to the magnetic field of the earth. His results were inconclusive and the experiment was soon abandoned. The effect of disturbances, such as motor-electrolytic actions, was in his case probably excessive, and the means to measure very small voltages inadequate at his time.

The experiments reported in this paper have been carried out on a smaller scale under laboratory conditions.

II. METHOD.

(1) *Arrangement.*—The experimental arrangement is shown in fig. 1. The fluid runs from a drum containing an indicating float through a rubber pipe to a flattened glass tube, which is placed in the airgap of an electro-magnet. The potential difference between two electrodes inserted into

* H. J. Northfield, *Electrician*, 1936, p. 40.

† G. W. O. Howe, *Electrician*, 1936, p. 14.

‡ In metals, the mobility of electrons is about 10^4 times greater (see Pohl, *Physical Principles of Electricity and Magnetism*, p. 250, 1930).

§ *Diary*, January, 12th to 14th, 1832.

the glass tube at right angles to the directions of flow and of magnetic field is measured.

The flow speed was determined by means of the level indicator and a

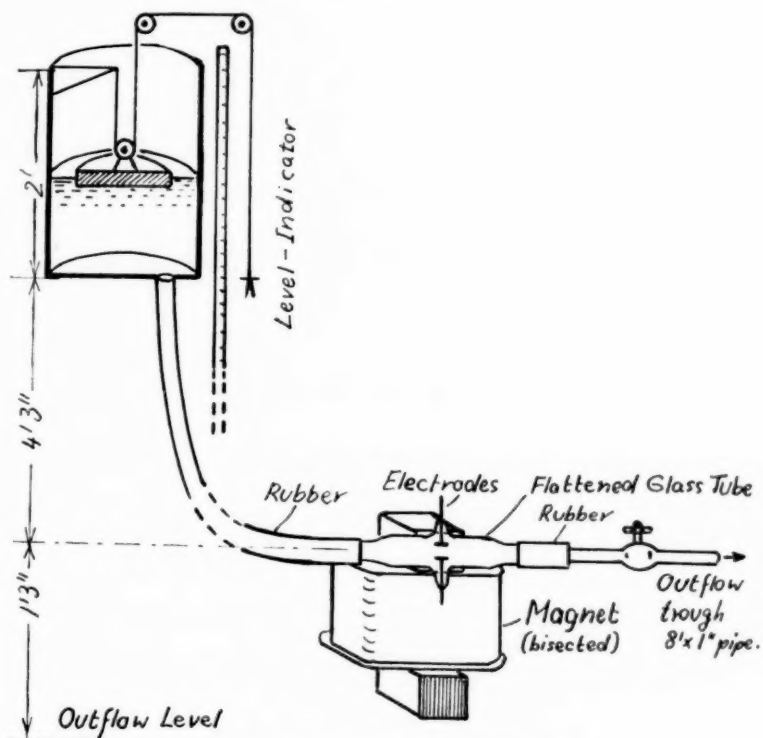


FIG. 1 (Container drawn to half the scale of magnet).

stop-watch, the cross-sectional areas of the drum (A) and of the flattened part of the glass tube (a) being known.

If the indicator travels the distance Δx cm. in Δt seconds, then the flow speed between the magnet jaws is

$$v = \frac{A}{2a} \frac{\Delta x}{\Delta t} = 90 \frac{\Delta x}{\Delta t}.$$

(From measurements $A = 1000 \text{ cm.}^2$; $a = 5.55 \text{ cm.}^2$.)

(2) *Reasons for Measuring Method adopted.*—The main difficulties foreseen are as follows:—

- (i) The voltages to be expected are small (a few millivolts), since the flow speed and the magnetic field intensity are limited.
- (ii) The internal resistance of this "low voltage generator" is high (a few thousand ohms). Therefore the amount of power available to feed an instrument is exceedingly small.
- (iii) Disturbances, such as electrolytic and motor-electrolytic effects threaten to supersede the electro-magnetic effect to be investigated.

These difficulties were overcome by employing an *A.C. Valve-Voltmeter* for measuring the E.M.Fs. and using an Alternating magnetic field. The Valve-Voltmeter combines the advantages of sensitivity and very small power consumption.

The use of an alternating field enables electrolytic effects to be eliminated* and facilitates the design of the Valve Voltmeter.

The drawback in using A.C. is that disturbing E.M.Fs. are induced in the Voltmeter leads (transformer effect), which have to be compensated.

(3) *Magnetic Field.*—The electro-magnet is fed from the 50 c/s municipal supply over isolating transformers in such a way that the mean potential level of the windings could be adjusted with respect to the earth potential. The field has been investigated by means of search coils, connected to the Valve Voltmeter, resp. to an oscillograph.

The field distribution along the flow axis is shown in fig. 7 (dotted line).

The time variation of the field is almost sinusoidal. A small third harmonic does not affect the flow induced voltage much; its disturbing effect by direct induction into the voltmeter circuit is discussed below.

(4) *Compensating of Transformer E.M.Fs.*—A difficulty due to the use of an A.C. Field has been mentioned above; the voltmeter leads act as the secondary of a transformer and voltages are induced which have to be eliminated. Two methods are possible.

(a) The voltmeter leads are arranged in such a way as not to enclose any flux. That means taking one connection up the airgap and making it mechanically adjustable. The occupation of valuable airgap space by connection leads is a disadvantage, of course, otherwise this solution has proved to be simple and practicable.

(b) Two leads are connected to the one electrode, one being taken out on each side of the magnet; they are shorted over a resistance, and the

* As an additional safeguard against motor-electrolytic effects, silver electrodes, coated with silver chloride, were used for the greater part of the experiments (see Newbery and Smith, Trans. Electrochemical Society, vol. 73, 1938, p. 266).

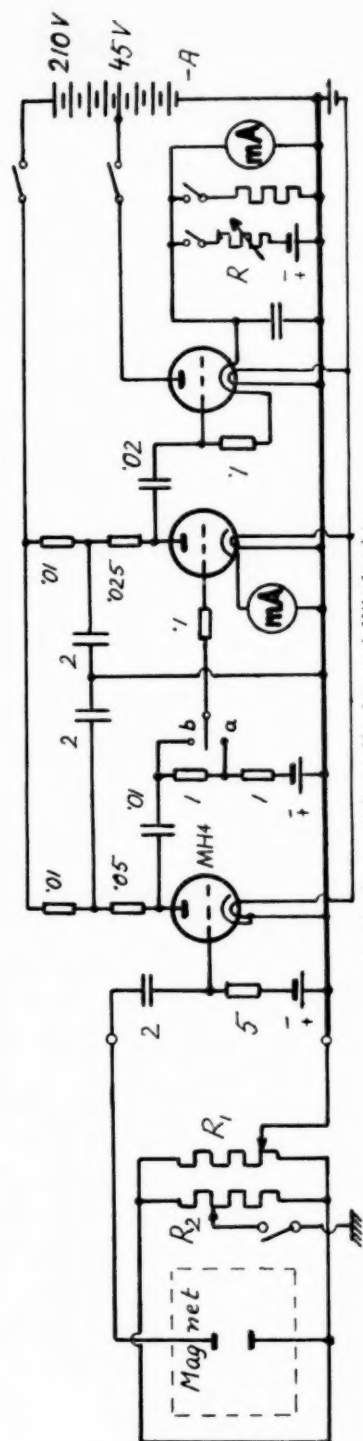


FIG. 2A (Figures indicate Megohms and Mikrofarads).

voltmeter terminal is connected to the rheostat slider, which is adjusted to obtain compensation (see fig. 2A). This method does not waste airgap space. For explanation see Appendix I.

(5) *Valve Voltmeter and Harmonics*.—A battery valve voltmeter consisting of two amplifier stages and one grid rectifier (fig. 2A) is employed to measure the induced voltages.

With a matching resistance of 5 megohms, the power absorbed with the instrument is negligible.

The sensitivity as seen from the calibration curves (fig. 2B) is well adapted to the expected voltage range.

A better approach to linearity may be achieved by employing three amplifier stages and a rectifier instrument or anode rectifier, but the

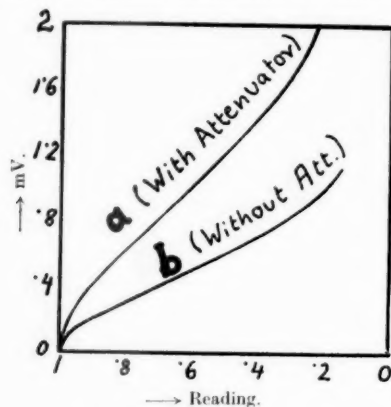


FIG. 2B.—Calibration Curve.

arrangement used safeguards against over-load, as the incremental deflection of the indicating milliammeter decreases with increasing applied voltage.

The calibration was carried out with a sinusoidal 50 c/s voltage and the flow induced voltage is also practically sinusoidal. But it was found that a third harmonic (i.e. 150 c/s) voltage of about .08 mV appears across the valve voltmeter terminals when the magnet is switched on, which could not be eliminated by compensation. Its value is independent of the flow speed, but as it is superimposed on the flow induced voltages it is apt to falsify the results unless a correction is made. To do this on grounds of theoretical consideration is hardly possible as the grid rectifier instrument reads neither RMS nor peak nor average values. The following experimental way was adopted:—

Non-sinusoidal waves of *known* composition supplied from two independent 50 and 150 c/s sources were applied to the valve voltmeter and the influence of the third harmonic on the reading noted. The measured results were then corrected accordingly.

The phase angle of the harmonic had to be considered and was ascertained by means of the oscillograph.

(6) *Procedure and Computations.*—The valve voltmeter is switched on, the zero position adjusted (by means of resistance R, fig. 2A). Then the magnet is switched on and a minimum deflection obtained by means of resistances R_1 and R_2 (in fig. 2A), *i.e.* the transformer E.M.F.s. are compensated out, but for the mentioned third harmonic. After opening the water-tap a reading was taken, and after closing it compensation and zero adjustment checked up.

Although the valve voltmeter does not take any appreciable current the voltage measured is bound to be smaller than the E.M.F. generated, on account of circulating currents, which constitute a kind of internal loading. An estimate of the influence of internal circulating currents and of double-earthing on the terminal voltage is made in Appendixes 2 and 3.

III. RESULTS.

(1) *Flow Speed; Magnetic Field; Electrode Distance.*—The main conclusion can be stated in advance as follows: In contradiction to some doubts mentioned at the outset, the E.M.F. induced in flowing water is just as in metallic conductors:

$$E = \int_0^l B v \, dl \times 10^{-8} \text{ volts,}$$

where dl is an element of path between the electrodes in cm., B the magnetic flux density in gauss, v the flow speed in cm./sec.

Considering that in the arrangement investigated, B and v are practically constant in space between the electrodes, the induced E.M.F. is simply

$$E = B l v 10^{-8}.$$

If B is alternating with time, E will be alternating too and of similar wave form.

A voltage V , equal to this E.M.F. diminished by internal voltage drops, can be measured

$$V = E k_1 k_2,$$

where k_1 and k_2 are correction factors, slightly smaller than 1, to allow for the voltage drop due to internal circulating currents (k_1) and due to double earthing (k_2). They can be estimated mathematically (see

Appendixes 2 and 3) and are independent of B and v , but vary slightly with l .

The measured voltage should therefore be proportional to the field and to the speed. The following experimental results corroborate these statements:—

(a) The induced voltage is directly proportional to the flow speed. This relation was established for different electrodes, different magnetic

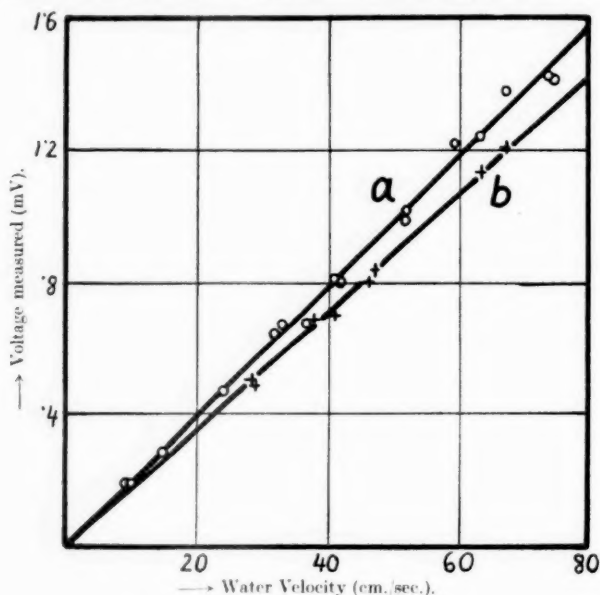


FIG. 3.—Induced Voltage and Flow Speed.

(a) 8 mm. electrodes on bare rods.

(b) 8 mm. electrodes on insulated rods.

2.5 cm. apart. $B=800$ Gauss.

fields, different fluids, and different electrode distances for speeds from 10 to 80 cm./sec. The graph, fig. 3, shows two typical sets of readings (the difference between the two lines is explained below, III, (4)).

(b) The induced voltage is proportional to the mean field intensity (fig. 4A). Each voltage-speed ratio value in figs. 4A and 4B is the mean value of a series of measurements at different speeds (slope of line in fig. 3; the inaccuracy is due to the inaccuracy of the field measurements).

(c) The induced voltage is very nearly proportional to the electrode spacing (fig. 4B). A perfect proportionality was not expected.

(d) *Quantitative Relations.*—In order to verify the above statement quantitatively, let us compare a calculated and measured voltage value

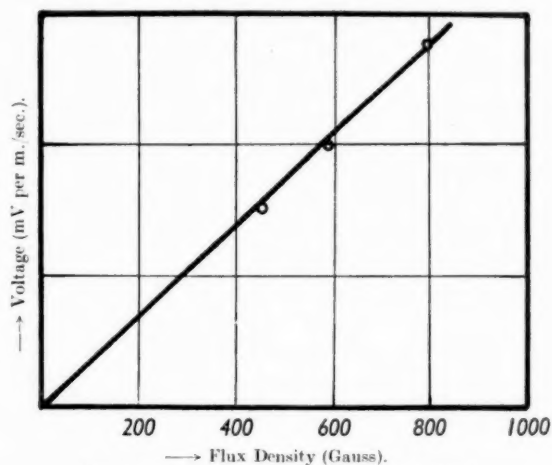


FIG. 4A.—Induced Voltage and Magnetic Field.
8 mm. Electrodes on insulated rods, 1.95 cm. apart.

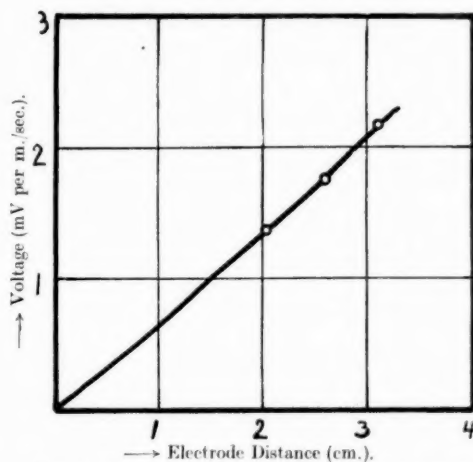


FIG. 4B.—Induced Voltage and Electrode Distance.
8 mm. Electrodes on insulated rods. $B = 800$ Gauss.

for the following data: $B = 800$ gauss; $v = 50$ cm./sec.; $l = 2.5$ cm. Hence $E = 1.00$ mV.

Circulating currents cause a voltage drop of 5 per cent. (see Appendix 2), hence $k_1 = .95$. To allow for double earthing in the case of small electrodes, 2.5 cm. apart, a correction factor $k_2 = .90$ is appropriate (see Appendix 3). Hence $V = .86$ mV.

The measured voltage (see fig. 3, curve *b*) is $V = .88$ mV. The two values agree well within the accuracy achieved. The disagreement may, moreover, be explained by a slight excess of water speed between the electrodes over the average velocity on which the calculation is based.

This clears up the main questions asked at the outset; but various other matters suggested themselves for investigation.

(2) *Conductivity*.—Comparative tests with tap water of 17,000 ohm cm., and a salt solution (NaCl) of only 200 ohm cm. specific resistance, show that the conductivity of the fluid does *not* influence the induced voltage, which is measured between the electrodes.

This verifies the theoretical result (Appendix 2) that the voltage drop due to *internal* circulating currents is independent of the conductivity. If an *external* load is applied, on the other hand, the terminal voltage is reduced and varies with the conductivity.

(3) *Position of Electrodes in Magnet Field*.—The question was asked: How does the relative position of the electrodes and the magnet affect the measured voltage? It is to be expected that the voltage picked up at the edge of the field is smaller than that at the centre. But it has to be determined whether there is any difference between a displacement of the electrodes upstream or downstream with respect to the centre of the magnetic field.

For very high speeds and high conductivity fluids (say mercury) the magnetic field should be distorted * by the circulating currents so as to be virtually shifted downstream (an analogy to the "armature reaction" in machines). But a quantitative estimate shows that this effect is exceedingly small in the present case where the speeds of flow are moderate and the resistivity high.

Another thought will be: Is there any lag in establishing an electric field, or will the charges be separated immediately the fluid enters the field? A trend of thought similar to that outlined in the introduction may lead to the fallacy that the sluggishness of the ions may cause some lag, but the experiment showed (within the limits of the accuracy achieved) that for a given displacement it makes no difference whether the electrodes are displaced upstream or downstream.

(4) *Different Electrodes*.—The following figures when studied in con-

* This effect in a 2-mm. copper plate is extensively treated in H. Hertz' thesis on "Induction in Rotating Spheres" (fig. 11, *a* and *b*). But the conductivity is there 10^9 greater than in our case.

junction with the electric field distribution (fig. 7) represent an additional, though rough, experimental check on the calculations in Appendix 2.

Measurements were made with the following electrodes:—

- (A) Round Silver—silver chloride—Disks (8 mm. diam.) at the end of $1\frac{1}{2}$ -mm. silver rods, the rods insulated by a shellac coating.
- (B) Same as (A) but rods bare.
- (C) Flat Silver—silver chloride—Plates (55 mm. \times 10 mm.) at the end of 1-mm. bare silver rods.
- (D) Brass Plates (55 mm. \times 10 mm.), both ends slightly bent up, on bare brass rods.

The following voltages have been measured with the electrodes 2.5 cm. apart, at 800 gauss; a corrected value (see Appendix 3) is also given to allow for the influence of double earthing:—

Electrode.	A.	B.	C.	D.
Voltage per 1 m. per sec. accer. veloc.	1.77	2.02	1.67	1.77 mV.
Corrected voltage per 1 m. per sec.	1.97	2.25	1.77	1.88 mV.

The electrodes (A) do not distort the electric field, and the voltage between two points of the flow space is picked up correctly to be compared with calculated values.

With electrodes (B) a higher voltage is obtained as the electrode distance is virtually increased (see also fig. 3).

With electrodes (C) and (D) a smaller voltage is measured, partly because the influence of the rods is relatively smaller, partly because the increased circulating currents from the ends of the plates, which extend into regions of smaller magnetic field, cause a higher internal voltage drop.

The difference between (C) and (D) is mainly due to increased flow speed between the electrodes in the case of (D), but the fact that the bent-up electrodes lie more or less in an equipotential line of the undistorted field (see fig. 7, Appendix 2) may also influence the result.

It should be noted for practical applications that small electrodes pick up larger voltages than extended ones.

(5) *Oscillography*.—By converting the grid rectifier part of the valve voltmeter into an additional amplifier stage and feeding over a 22 : 1 step-down transformer into a Duddell type oscillograph, oscillograms have been taken with a 100 mA loop (if a more sensitive loop had been available, a series resistance could have been used in place of the transformer).

The curves revealed the disturbances which could not be eliminated, as third harmonics, and by also showing their phase angle indicated the proper way of correcting the results.

The flow voltages themselves proved to be pretty nearly sinusoidal, the

harmonics in the magnetic field being small. Oscillograms of water surges are discussed below.

IV. PRACTICAL APPLICATIONS.

Although the experimental arrangement constitutes the purest form of a hydro-electric generator, any power applications are out of the question, mainly on account of the high resistivity of electrolytes and the resulting low efficiency; the difficulty of adding up the small voltages gained (problem of the unipolar machine) is a further drawback.

There is a greater scope in the field of measurement. As the voltage is proportional to the speed and independent of conductivity fluctuations,

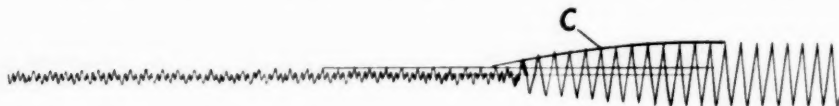


FIG. 5A.

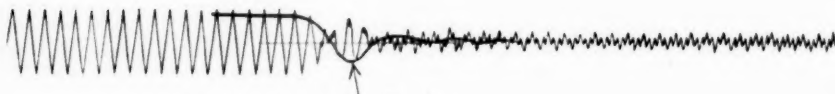


FIG. 5B.

the development of an electro-magnetic flow speed indicator is possible; but it would hardly be competitive in cases where simpler and more direct methods exist.

There remains one sphere where the electric magnetic measuring method may prove extremely useful: the investigation of *varying* water speeds. The well-developed technique of electric oscillography can be applied to hydraulic problems such as water-hammer, valve actions, instabilities of flow, etc.

To show this a number of oscillograms have been taken while releasing or stopping a water-flow. Fig. 5A shows the sudden release of the water column in the experimental flow circuit (fig. 1).

A mathematical analysis assuming the friction to vary with the square of the speed shows that the relation between speed (v) and time (t) should be $v = v_{\max} \tanh Bt$; the coefficient B has to be determined from the dimensions of the flow circuit. The calculated curve (c in fig. 5) agrees very well with the measured rate of speed increase.

Fig. 5B shows the effect of stopping water-flow suddenly. Surging back is clearly seen at the instant indicated by the arrow. Reversal of flow is

proved by the 180-degree phase shift of the induced voltage. The residual wave-line after stopping, partly due to poor compensation, partly due to the third harmonic, affects the appearance of the oscillogram more than its value for evaluation.

The main object of these oscillograms, taken without great preparation, is to show the possibilities of the method for the investigation of hydraulic transients.

V. CONCLUSIONS.

The induced E.M.F. is proportional to the speed, the magnetic induction, and practically proportional to the length of conducting path. The measurable voltage is reduced by an internal voltage drop, but as it is still proportional to the speed and independent of the conductivity, an electro-magnetic method of measuring flow speeds is possible. The electrodes should be made small for best sensitivity. Oscillography of the induced voltages in a moving fluid may open a field of research on hydraulic transient phenomena.

Grateful acknowledgment is made to the Research Grant Board which financed the experiments carried out. Thanks are also due to Professor B. L. Goodlet, Mr. N. H. Roberts, and Dr. R. Guelke, for helpful advice.

APPENDIX I.

On Transformer E.M.F.s.

The left-hand side of fig. 2A can be redrawn as in fig. 6.

If E_1 , E_2 are the E.M.F.s. induced in each section of the circuit and R_1

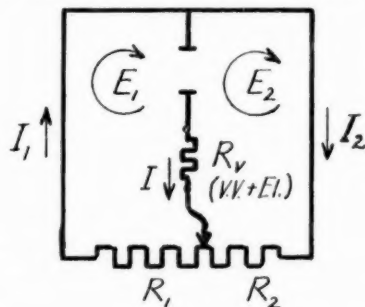


FIG. 6.

and R_2 the respective rheostat sections, R_v the voltmeter resistance, including the resistance between the electrodes, the currents I_1 , I_2 , I as shown, then

$$\begin{aligned} E_1 &= I_1 R_1 + I R_v, \\ E_2 &= I_2 R_2 - I R_v, \\ I &= I_1 - I_2. \end{aligned}$$

Eliminating I_1 and I_2 and solving for I :

$$I = \frac{E_1 R_2 - E_2 R_1}{R_e(R_1 + R_2) + R_1 R_2}.$$

Now if $R_e \gg R_1$ and R_2

$$IR_v = \frac{E_1 R_2 - E_2 R_1}{R_1 + R_2}.$$

This is the voltage measured due to transformer E.M.Fs.

It can be made zero by making $R_1/R_2 = E_1/E_2$.

APPENDIX 2.

Calculation of Circulating Currents.

The electric field induced in the moving medium causes currents to circulate.

A knowledge of these currents is desirable in order to estimate the internal voltage drop and to gain knowledge about the actual physical electric field.

The following assumptions are made:—

- (1) The magnetic field does not vary with time.
- (2) It does not vary in its own direction, the Z-axis.
- (3) Otherwise its space distribution is given by a double Fourier Series * for E_0 modified by the velocity distribution.
- (4) The fluid flows only in the direction of the positive x-axis.
- (5) The current flow region is terminated by four planes $y = \pm b$ and $z = \pm d$, which form insulating boundaries.
- (6) External currents, e.g. due to double-earthing or voltmeter load, are not considered.

Assumptions (2), (4), and (5) reduce the problem to a two-dimensional one.

Notation.—

E = Intensity of electric field.

E_0 = Intensity of externally induced field = $Bv10^{-8}$.

i = Current density.

A, B, C, P, Q, coefficients of Fourier Series.

l, b = Length and breadth of flow space.

$p = \pi/2l$ and $q = \pi/2b$.

k = Conductivity.

Fundamental Equations.—

From Assumption (1) follows:

$$\text{curl } E = 0 = \frac{\partial E_x}{\partial y} - \frac{\partial E_y}{\partial x}. \quad (1)$$

From Assumption (2) follows:

$$\text{div } i = 0 = \frac{\partial i_x}{\partial x} + \frac{\partial i_y}{\partial y}. \quad (2)$$

* See H. Hertz, *Induction in Rotating Spheres*, Misc. Papers, 1896, p. 55.

Further on:

$$\mathbf{E}_x = \frac{\mathbf{I}_x}{k} \quad \text{and} \quad \mathbf{E}_y = \frac{\mathbf{I}_y}{k} + \mathbf{E}_0. \quad (3)$$

Let the distribution of the externally induced field \mathbf{E}_0 be:

$$\mathbf{E}_0 = E' \sum_m A_m \cos mpx \times \sum_n B_n \cos nqy, \quad (4)$$

where $m = 0, 1, 2, 3, \dots$ $n = 1, 3, 5, 7, \dots$

There can be no sin terms as the field is symmetrical. There are no even harmonics in the y direction in order to make the field between the lines $y=b$ and $y=2b$ an image of the field between $y=0$ and $y=b$.

The coefficients A and B are chosen to reproduce the true distribution of the magnetic field as near as possible.

Multiplying (5) out, one obtains:

$$\mathbf{E}_0 = E' \sum_{mn} Q_{mn} \cos mpx \cdot \cos nqy. \quad (5)$$

Solution.—Let the two components of the current density in the direction of the x and y axis be:

$$\mathbf{I}_x = kE' \sum_{mn} P_{mn} \sin mpx \sin nqy$$

and
$$\mathbf{I}_y = kE' \sum_{mn} Q_{mn} \cos mpx \cos nqy. \quad (6)$$

Differentiating (6) and substituting in (2) yields one set of equations for the Fourier Coefficients:

$$mpP_{mn} = nqQ_{mn}, \quad (7)$$

and substituting (6) in (3), differentiating suitably and substituting in (1) another set:

$$nqP_{mn} + mpQ_{mn} = -mpC_{mn}. \quad (8)$$

From (7) and (8) the coefficients P and Q are readily obtained:

$$P_{mn} = \frac{-C_{mn}}{\frac{pm}{qn} + \frac{qn}{pm}} \quad \text{and} \quad Q_{mn} = \frac{-C_{mn}}{1 + \left(\frac{nq}{mp}\right)^2}. \quad (9)$$

By substituting (9) in (6) the current density at any point is obtained.

A system of current lines can be calculated by means of a simple integration as

$$\mathbf{I} = kE' \sum_{mn} \frac{Q_{mn}}{mp} \sin mpx \cos nqy, \quad (10)$$

where the line $\mathbf{I}=0$ passes the origin $x=0, y=0$.

Equipotential lines are also obtained by integration as

$$\mathbf{V} = -E' \sum_{mn} \frac{C_{mn} + Q_{mn}}{nq} \cos mpx \sin nqy, \quad (11)$$

where the potential along the line $y=0$ is zero.

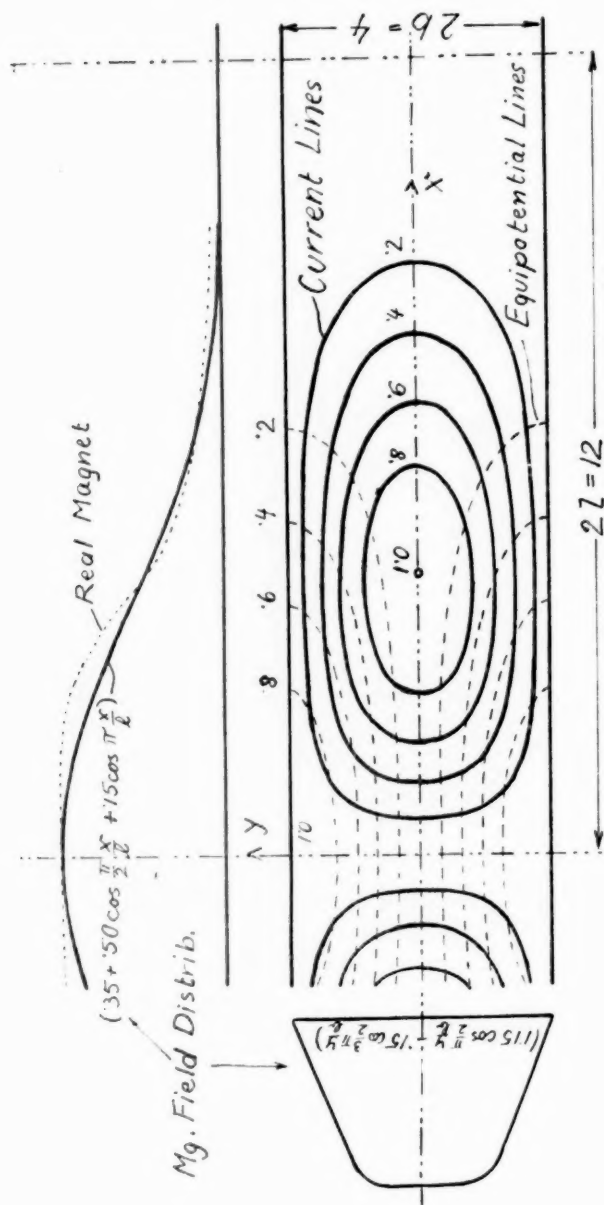


FIG. 7.

The voltage drop due to circulating currents is given by Q_{mn} which is negative (see equation 9).

It is independent of the conductivity.

Numerical Example.—Current and equipotential lines are calculated for a simplified field distribution,

$$B = B_{\max}(\cdot 35 + \cdot 50 \cos px + \cdot 15 \cos 2px)(1 \cdot 15 \cos qy - \cdot 15 \cos 3qy),$$

where $p = \pi/12$ cm. and $q = \pi/4$ cm., and the result is pictured in fig. 7.

The voltage drop at the magnet centre would be about 9 per cent. By taking a greater number of harmonics into account, a voltage drop of about 5 per cent. has been determined for a distribution very near to the one in the experiment.

APPENDIX 3.

Correction for Error introduced by Double-earthing.

There are two types of circulating currents causing an internal voltage drop, with the effect that the measurable voltage is smaller than the E.M.F.

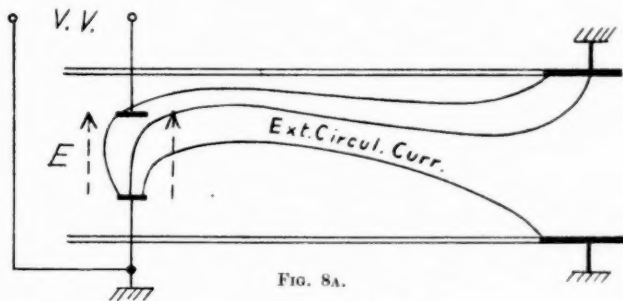


FIG. 8A.

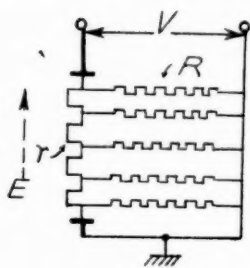


FIG. 8B.

First, there are internal circulating currents within the fluid (see Appendix 2); second, there are external circulating currents due to double-earthing.

To earth certain parts of the fluid circuit, particularly the outflow tubing, is inevitable, and earthing one lead of the V.V. was found advisable to prevent disturbing waves being picked up or deflections being caused by touching parts of the circuit.

The problem is depicted in fig. 8A. An accurate calculation of the quasi-stationary current flow similar to that carried out for the internal circulating currents would offer considerable difficulties. The reduction in terminal voltage is therefore assessed by means of the equivalent circuit shown in fig. 8B on the basis of resistance measurements.

If the E.M.F., induced linearly between the electrodes, is E , a voltage

$$V = \frac{E}{r/R_v + \sqrt{r/R} \cot h \sqrt{r/R}}$$

will be measured, where R_v is the voltmeter resistance, while the values for r and R have to be chosen to suit the measured resistance values according to the following equations:—

$$\text{Resistance between electrodes} = 2\sqrt{rR} \tan h \frac{1}{2}\sqrt{r/R}.$$

$$\text{Resistance from one electrode to earth} = \sqrt{rR} \cot h \sqrt{r/R}.$$

Some resistance values and correction factors V/E , for $R_v = 5\text{M}\Omega \simeq \infty$, are given in the following table:—

Electrodes . . .	55 mm. flat. 2.5 cm.	8 mm. round. 2.5 cm.	8 mm. round. 2 cm.
El. distance . . .			
Resistance measured			
between electrodes . . .	4000	10000	8200
between one electrode and earth	24000	32000	32000
between both electrodes and earth	23000	30000	30000
Calculated resistance r . . .	4100	10200	8400
" " R . . .	22500	29000	29000
Correction factor (k_2)94	.90	.91 ₅

A PRELIMINARY ACCOUNT OF RAINFALL IN JONKERSHOEK.

By C. L. WICHT, Forest Research Officer.

(With four Text-figures.)

(Read October 18, 1939.)

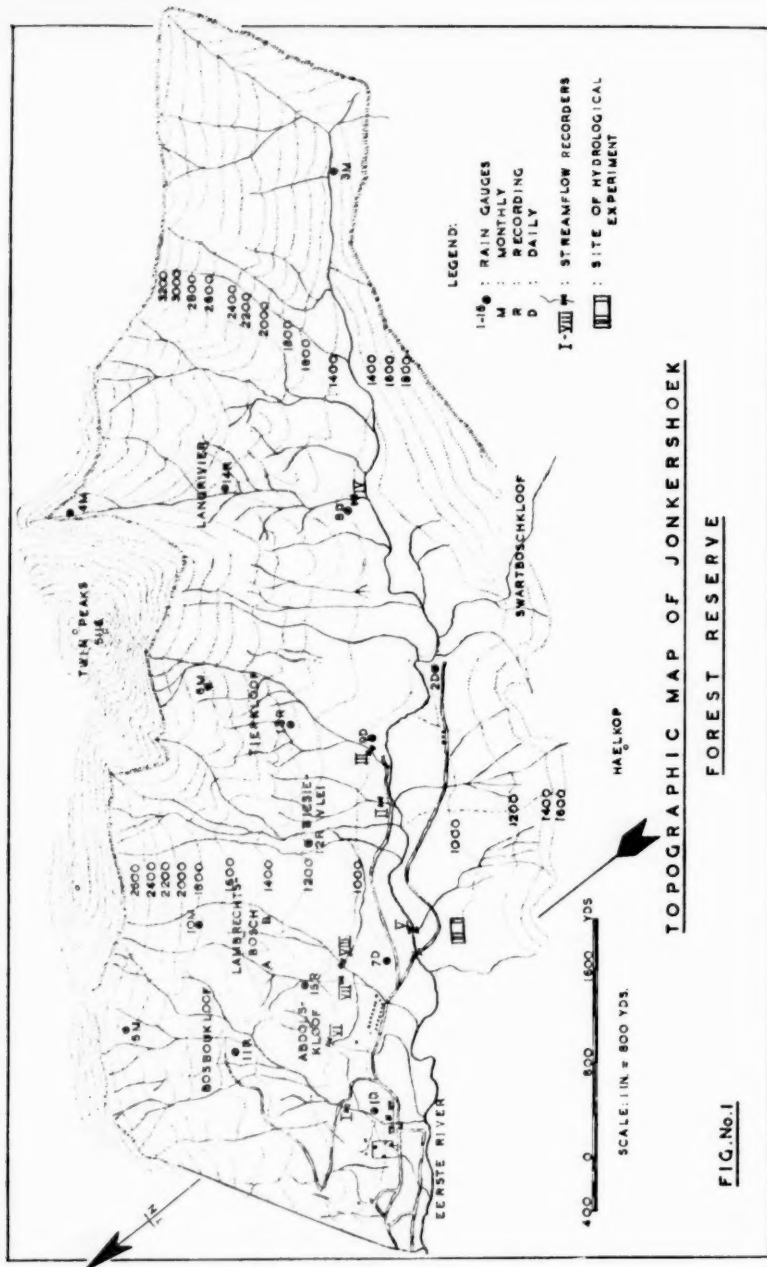
The rainfall at the Jonkershoek Forest Research Station is being studied intensively in connection with the investigation of the effects of forests on water conservation. Rainfall data from the mountains of the Cape are so rare, however, that they are interesting to botanists, zoologists, meteorologists, and other scientists, irrespective of the purpose for which they are being collected. Civil and irrigation engineers, who are dependent on the mountain streams for their water supplies, find detailed records of the amount, intensity, and distribution of precipitation in the mountains particularly valuable. A separate presentation of the large amount of data which is beginning to accumulate at Jonkershoek appears to be justified therefore, and this paper is intended to pave the way for later accounts of the rainfall in this area. The paper deals only with data available up to the end of 1938.

The main features of rainfall which will be considered are the total annual precipitation, the monthly and seasonal distribution of precipitation, and the intensity and duration of showers.

A brief general description of the topography, climate, and situation of the research area will be given first, however, because the peculiarities of the rainfall are difficult to understand without it.

DESCRIPTION OF SITUATION, TOPOGRAPHY, AND CLIMATE OF JONKERSHOEK.

The Jonkershoek Forest Reserve is situated five miles to the south-east of Stellenbosch. It comprises the end of a long narrow valley, which has been eroded along a line of faulting by the Eerste River. The "Hoek" is elongated in a north-west to south-east direction and is cut off by high precipitous mountains to the north-east, south-east, and south-west so that a cul-de-sac is formed. The tops of the mountains are from 4000 to 5000 feet high and consist of almost bare siliceous Table Mountain Sandstone. The lower slopes, falling down to the river, are composed of Table Mountain



Sandstone talus overlying granite, or Frenschhoek Shales where these have not been absorbed by the intruded granite. These slopes are covered with typical proteaceous shrub vegetation except where small forest remnants still exist along stream beds. Fig. 1 is a contour map of these slopes. This map has been adapted from one prepared by Forester P. A. Grobler in 1934.

The region enjoys a humid, temperate, winter rainfall climate, which is typical of the south-western Cape. In winter the prevailing rain-bringing winds blow from the north-west directly into the entrance of Jonkershoek, which acts as an effective rain-trap. In summer the prevailing winds are from the south-east. These winds are dry in the valley. They bring only orographical rains to the mountain-tops. The local topography makes it practically impossible for wind to blow in any other direction. Winds from other points of the compass blow over the valley and are not felt in it.

The high mountain-tops normally experience falls of hail and snow two or three times every winter. On rare occasions some of the rain-gauges situated at higher altitudes in Jonkershoek receive small quantities of this type of precipitation.

THE METHODS OF INVESTIGATING RAINFALL IN JONKERSHOEK.

Fifteen permanent rain-gauges have been erected on an area of about 4000 acres. Their positions have been marked on the topographic map (fig. 1). The gauges 1, 2, 7, 8, and 9 are relatively easily accessible and are read every morning when rain has occurred. They are standard five-inch gauges mounted four feet above the ground, as prescribed for all gauges of the Meteorological Office. The gauges 11, 12, 13, 14, and 15 are weekly Casella Siphon Rainfall Recorders with eight-inch funnels. These gauges have an unlimited capacity, because an automatic siphon empties the float-well after $\cdot 4$ of an inch of rain has been received. All water siphoned over is caught in a can and the quantity is checked in a measuring-glass. These recorders operate satisfactorily if the float-well and siphon are cleaned carefully every week. The siphon easily becomes clogged if dust and other solid matter is allowed to accumulate in the apparatus. These gauges record the time of commencement, duration, and amount of each shower. The gauges 3, 4, 5, 6, and 10 are situated on inaccessible sites and are read monthly. They are standard five-inch gauges with large containers in which the rainfall received during the month accumulates. To prevent evaporation fifteen pints of liquid paraffin are introduced into each container each month. The paraffin being lighter than water then forms a protective layer over it.

The gauges 1, 2, 3, and 4 have been kindly provided by the Chief Meteorologist.

In addition to the permanent gauges which have been mentioned, temporary rain-gauges will be established in connection with special investigations. The data from these will supplement the routine readings.

The most serious errors in the rainfall records obtained by the standard-gauging technique which has been described are probably due to differences in the exposure of the gauges to wind (Mead, 1919, p. 189; Hann and Süring, 1926, p. 334; Schaffernak, 1935, p. 15; Kleinschmidt, 1935, p. 283). Hellman found (Hellman, 1892, quoted by Zon, 1927) that an ordinary rain-gauge may register 19 per cent. less rainfall than actually falls in a wind of medium velocity. In two cases in Jonkershoek, gauges set about 150 yards apart have shown constant differences in rainfall on otherwise apparently uniform sites. As these sites will be required for intensive hydrological research, various methods of screening the gauges are now being tested, in order to ascertain whether the differences recorded are due to actual differences in the amounts of precipitation.

ANALYSIS OF THE AVAILABLE RAINFALL DATA.

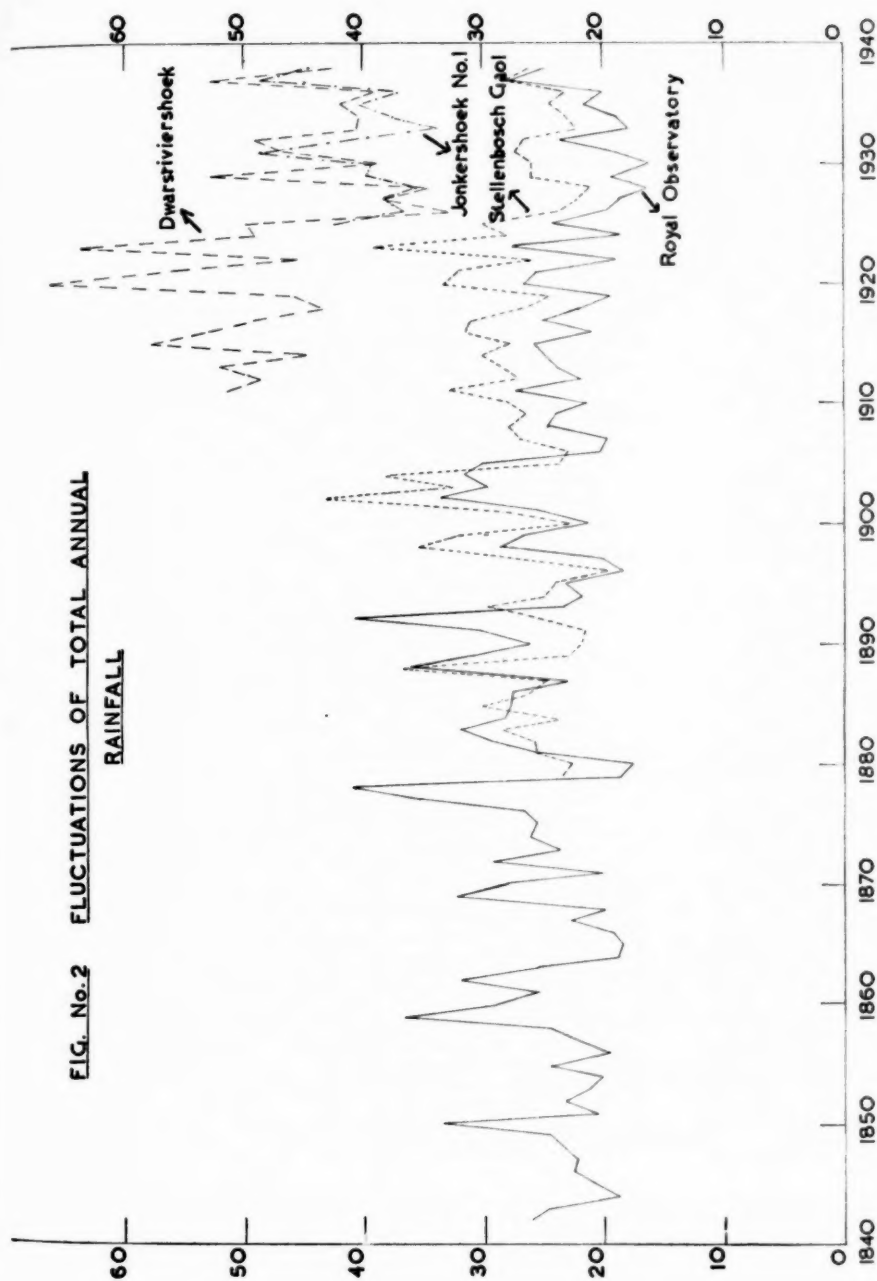
The Jonkershoek rain-gauge No. 1 has been read since 1925. All other gauges on the area have been established since the inauguration of the research scheme in 1935. The period of observation is short, and it is necessary, therefore, to compare the available rainfall data with the records of other gauges in this rainfall region in order to judge their true significance.

THE TOTAL ANNUAL PRECIPITATION.

The average total annual precipitation recorded by gauge No. 1 from 1925 to 1938 is 40.64 inches. Other gauges in the Cape region which have been read for longer periods show, however, that the rainfall has been remarkably low since 1925 (Schumann and Thompson, 1934). The rainfall fluctuates very considerably from year to year at the Cape, which makes it difficult to recognise the general trends from the records. These annual fluctuations at four stations have been graphically demonstrated in fig. 2, from which it may be seen that a number of dry years were experienced after 1925. Smoothed curves are obtained if the "running means" (Tippett, p. 162, 1931) for ten-year periods are plotted instead of the annual totals. This has been done in fig. 3. The points of "running means" are calculated as follows: If x_1, x_2, \dots, x_n are the individual annual rainfall totals the running means are:

$$\begin{aligned} & \frac{1}{10}(x_1 + x_2 + x_3 \dots x_{10}), \\ & \frac{1}{10}(x_2 + x_3 + x_4 \dots x_{11}), \\ & \frac{1}{10}(x_{n-9} + x_{n-8} \dots x_n). \end{aligned}$$

FIG. No. 2 FLUCTUATIONS OF TOTAL ANNUAL
RAINFALL



The records at the Royal Observatory go back to 1842, and the smoothed curve for this station clearly shows a pronounced downward trend after about the period 1915-24. The lowest mean ever recorded was obtained for the period 1926-35. A similar trend is shown by the records from the Stellenbosch Gaol, which is situated five miles from Jonkershoek No. 1. The lowest mean on record at this centre was obtained for the period 1927-36. The data for the Royal Observatory and the Stellenbosch Gaol were kindly supplied by the Chief Meteorologist. Records, kindly provided by Mr. A. C. Buller from a gauge on his farm Dwarsriviershoek, also reflect this characteristic drop in the amount of annual precipitation. This farm is situated in the Banghoek, a valley which is adjacent to Jonkershoek and resembles it in topography. It may be concluded, therefore, that the calculated average for Jonkershoek would probably have been five or more inches higher had the records covered a longer period.

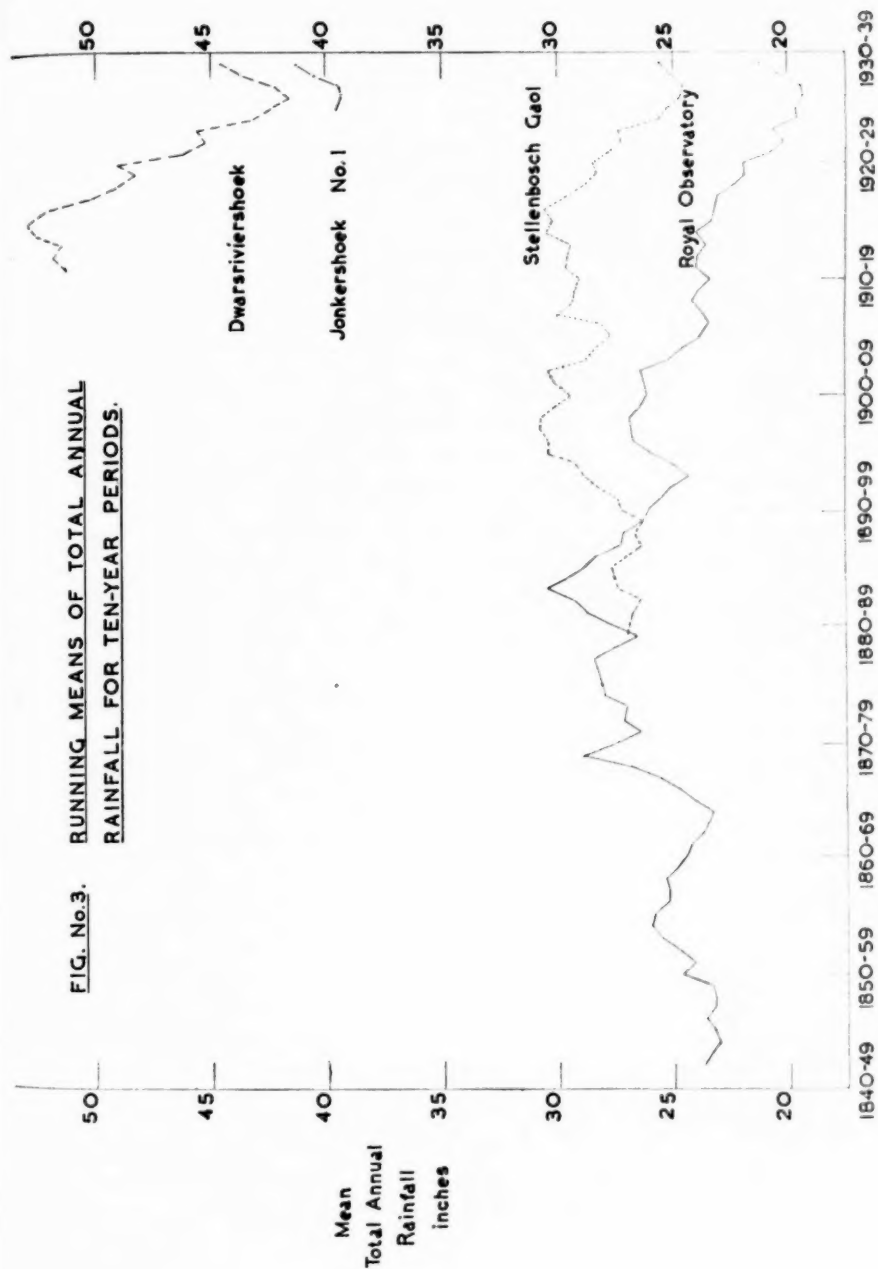
The mountain complex into which Jonkershoek cuts is characterised by very high rainfall. On the rainfall map of the Union published in 1925 (Rainfall Normals, 1925) the mountains are shown as receiving over 100 inches per year, which is the highest total annual precipitation recorded in the Union of South Africa. The rise in the amount of precipitation received, which occurs as one proceeds into the mountains and up to higher altitudes, is clearly shown by records from Jonkershoek. Table I shows that the precipitation at Gauge No. 1 is nearly double that received at

TABLE I.

Year.	Stell. Gaol.	Numbers of Jonkershoek Rain-gauges.											
		1.	2.	3.	4.	5.	6.	7.	8.	9.	11.	12.	13.
1925	30-31	42-75											
1926	24-02	36-75											
1927	22-44	38-38											
1928	21-27	35-65											
1929	26-17	39-81											
1930	26-17	39-59											
1931	27-60	48-55											
1932	26-94	43-78											
1933	22-43	33-87											
1934	23-45	37-26											
1935	24-68	40-17											
1936	23-41	37-09	53-77	77-38									
1937	28-11	48-70	59-66	76-12	84-78	50-98	56-89	..	61-20	53-44	49-08		
1938	26-45	44-47	58-27	75-05	70-52	40-09	50-14	45-99	59-18	51-10	43-89	49-83	48-33

N.B.—The gauges 10, 14, and 15 have not yet been read for a complete calendar year.

FIG. No.3. RUNNING MEANS OF TOTAL ANNUAL RAINFALL FOR TEN-YEAR PERIODS.



Stellenbosch Gaol, only five miles away, and at Gauge No. 3, another five miles farther into the valley, the precipitation is nearly doubled again.

The distribution of these gauges is shown on the Topographic Map (fig. 1), and an examination of Table I together with the map at once reveals the existence of a correlation between rainfall, altitude, and distance into the valley to the south-east. Gauge No. 1 near the north-west end of the reserve and almost at the lowest point in the valley must record very nearly the lowest precipitation on the area.

During 1937 a temporary gauge was maintained on the mountain to the south-east above Swartboschkloof. This gauge, which was situated on a site exposed to very strong wind, received 101.74 inches of precipitation. This phenomenally high rainfall contributes to the winter floods experienced by the Eerste River. The river is frequently converted within a few hours from a clear stream delivering ten cusecs (cubic feet per second) to a wild torrent delivering thousands of cusecs.

The annual fluctuation of rainfall at Jonkershoek Gauge No. 1 is less than at the Stellenbosch Gaol or at the Observatory. This is reflected by values of Pearson's Coefficient of Variation (Tippett, 1931, p. 25), which is a relative measure for the dispersal of observations about the mean. It is determined by expressing the "standard deviation" as a percentage of the mean. At Jonkershoek the mean is 40.64 inches; the standard deviation (μ) is ± 4.47 , and the Coefficient of Variation is 10.99 per cent. At Stellenbosch Gaol, where the mean is 27.73 inches and μ is ± 4.76 , it is 17.18 per cent. At the Royal Observatory, where the mean is 24.60 inches, and μ is ± 5.05 , it is 20.51 per cent. The reason for this increase is probably that it rains more easily in and near the mountains, and the total annual precipitation received in these parts is therefore more constant.

All the Jonkershoek gauges except possibly Nos. 1 and 4 are exposed to wind more or less, so that most of the records are no doubt too low. Over-exposure may account for the low readings of Nos. 5 and 11 in 1938 which are lower than the record from No. 1, although these gauges are situated at greater altitudes. In 1938 No. 13 also gave a lower record than No. 12, and both these gauges gave lower records than No. 9. Dr. Burger describes how rain-gauges in an afforested catchment in the Emmental, Switzerland, where they were sheltered from wind, showed an increase in precipitation with increase in altitude; and gauges in an adjacent bare catchment, which were exposed to wind, showed the reverse (Burger, 1931).

THE MONTHLY DISTRIBUTION OF RAINFALL.

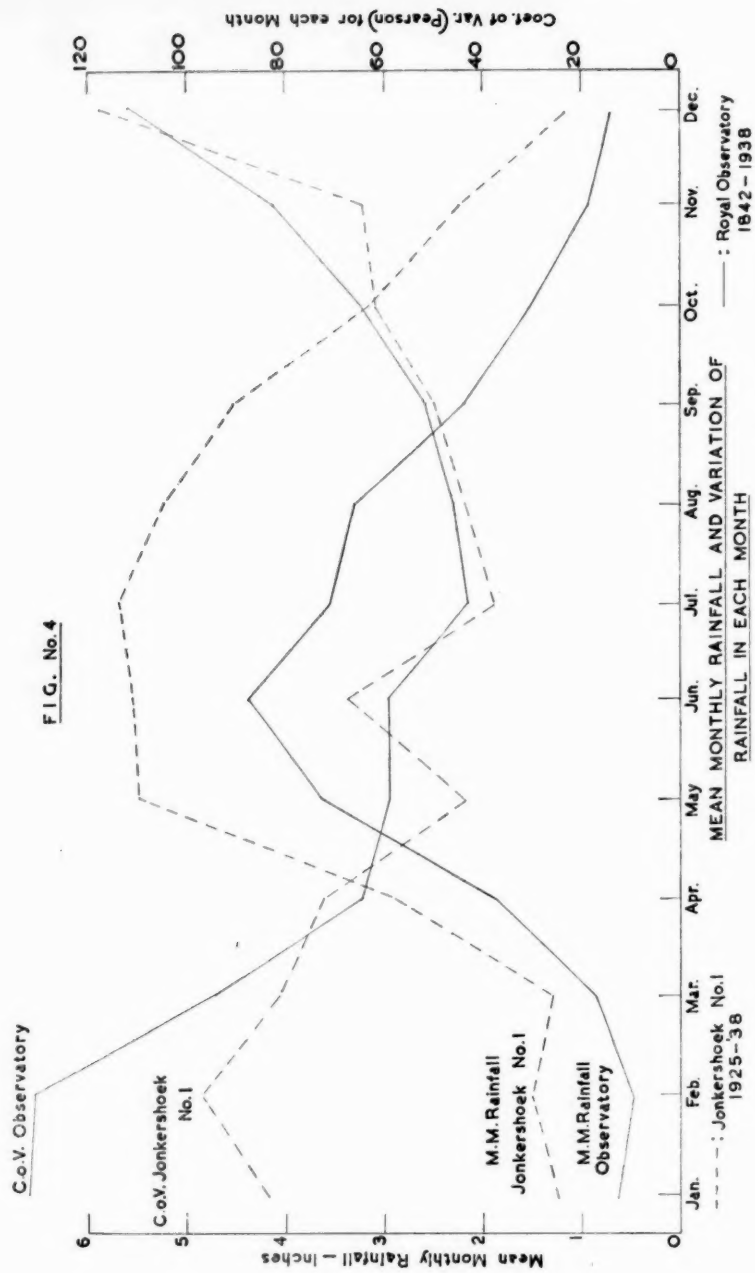
The mean monthly rainfall totals at Jonkershoek Gauge No. 1 for the period 1925-38 and at the Royal Observatory for the period 1842 to 1938

have been plotted in fig. 4. The curve, based on data from the Royal Observatory, demonstrates the fact that June is the wettest month over the western portion of the winter rainfall zone (Plummer, 1932). At Jonkershoek July has been the wettest month in the last fourteen years, but this may be an abnormality due to the short observation period. The wet winter months at both stations are clearly May, June, July, August, and possibly September. The dry summer months are November, December, January, February, and March. April, October, and perhaps September are transition months. On the average over 60 per cent. of the total annual precipitation was received in the four true winter months at the Royal Observatory. At Jonkershoek since 1925 about 55 per cent. of the mean total annual downpour fell during these months. The seasonal and monthly distributions of rainfall in the south-western Cape have been analysed by Plummer (Plummer, 1932), and it is sufficient to say that the records for Jonkershoek Gauge No. 1 indicate trends similar to those disclosed by him for this region.

In addition to the distribution dealt with by Plummer, foresters and agriculturists are particularly concerned with the variation from year to year of the rainfall recorded for each month. They are interested to know whether the total amount of rainfall received from year to year is likely to deviate much from the calculated mean or not. The relative variation of the rainfall totals in the various months may be compared by making use of Pearson's Coefficient of Variation.

This coefficient has been calculated for each month and the results plotted in fig. 4. It is clear that the precipitation in the wet winter months is less likely to deviate from the average than in the dry summer months. If we confine our attention to the winter months we note that the rainfall in the relatively wet months May and June—they actually have the highest mean monthly totals at the Royal Observatory—is more variable than in July and August. The rainfall received in June at Jonkershoek has been particularly variable in the period of observation. The rainfall in the early winter months is, therefore, unreliable. These months may receive good rains or they may be very dry. Forest Officers should exercise care not to carry out planting operations when the soil shows a tendency to dry out after the first winter rains, because the newly planted trees may then not be able to survive a dry May or June. The danger of an abnormally dry July or August is not so great.

Other gauges in Jonkershoek receive greater amounts of precipitation than No. 1, but in general they probably show a monthly distribution similar to that recorded by it. The south-east winds bring summer rains to the tops of the mountains behind Jonkershoek every year, but this type of downpour seldom affects the summer records on the lower slopes



of the valley. These rains contributed to the very high total recorded by the temporary gauge maintained on the mountain during 1937.

South-east wind clouds are as prevalent on the Jonkershoek mountains as they are on Table Mountain. If observations of precipitation from these clouds, similar to those made by Marloth on Table Mountain, were made here, equally remarkable data would possibly be collected (Marloth, 1903 and 1905). Marloth found that if a number of reeds, one foot high, were fixed above an ordinary five-inch gauge, so that water condensing on these would drip into it, the precipitation recorded was 300-400 per cent. higher than that recorded by another gauge without twigs. In misty weather the difference in the records amounted to more than 1000 per cent.

In November 1936 an exceptional south-east rain occurred in Jonkershoek. Up to the 15th of that month Stellenbosch experienced dry summer weather with incessant south-east wind. Gauge No. 1 at Jonkershoek received 1.02 inches of rain in the form of a fine drizzle from the south-east. Gauge No. 2—3600 yards to the south-east—received 4.31 inches, and No. 3—7700 yards to the south-east of No. 1—received the phenomenal amount of 11.48 inches. This heavy rain caused the Eerste River to come down in heavy flood as it does in winter. This precipitation differed from that recorded by Marloth in that it occurred as rain and not as mist condensation. It was caught in a standard five-inch gauge.

THE INTENSITY AND DURATION OF SHOWERS.

The records of the intensity and duration of showers are as yet very incomplete due to the shortness of the observation period, and no detailed

TABLE II.
SUMMARY OF DATA YIELDED BY RECORDING RAIN-GAUGES NOS. 11,
12, AND 13.

Year.	Total Annual Rainfall, Inches.	Total Annual Duration, Hours and Minutes.	No. of Showers, per Year.	Average Amount per Shower, Inches.	Average Duration, Minutes.	Average Intensity, Inches per Hour.
No. 11						
1937	49.08	474 h. 50 m.	560	.088	51 m.	.104
1938	43.89	617 h. 55 m.	449	.098	83 m.	.071
No. 12						
1938	49.83	680 h. 55 m.	525	.095	78 m.	.073
No. 13						
1938	48.33	659 h. 15 m.	492	.098	80 m.	.074

analysis will be attempted at this stage. The available data has been summarised in Table II, however. The records for 1938 show that the greater the precipitation the greater are the total duration of downpour and the total number of showers. The average intensity of precipitation apparently increases to the south-east into the valley.

The heaviest downpour recorded so far occurred on the 14th to 16th May 1938. The precipitation received was as follows:—

TABLE III.

Gauge No.	Rainfall, Inches.	Number of Showers.	Total Duration.
14	4.80	20	30 h. 45 m.
13	4.58	30	28 h. 15 m.
12	4.05	28	31 h. 15 m.
11	3.10	29	24 h. 35 m.

The greater precipitation to the south-east was due to the higher intensity and longer total duration of downpour. At No. 14 showers separated by short intervals and recorded separately at No. 11 became merged so that a lower number of showers was recorded. When the downpour reached its peak two inches were received in about two hours at No. 14. At No. 11 only about one inch was received in the same time.

SUMMARY.

An intensive study of rainfall is being conducted in connection with forest hydrological research at the Jonkershoek Research Station, five miles to the south-east of Stellenbosch.

A topographic map of the Research Station is given, and its situation, topography, and climate are described briefly. The methods of observing rainfall, including the establishment of fifteen permanent rain-gauges, are dealt with. The greater portion of the paper is devoted to a preliminary analysis of the data on total annual precipitation, monthly and seasonable distribution of precipitation, and intensity and duration of showers.

REFERENCES.

1. BURGER, H. Wald klimafragen. Mitt. d. schw. Centralanstalt f.d.f. Versuchw. Bd. xvii, Ht. 1.
2. HANN-SÜRING. Lehrbuch der Meteorologie, 4th ed. Tauchnitz, Leipzig, 1926.
3. HELLMANN, G. "Resultate des Regennessungs, Versuchsfeldes bei Berlin, 1855 bis 1891," Met. Zeitsch., 1892.
4. KLEINSCHMIDT, E. Handbuch der Meteorologischen Instrumente. Julius Springer, Berlin, 1935.
5. MARLOTH, R. "Results of Experiments on Table Mountain for Ascertaining the Amount of Moisture deposited from South-east Clouds," Trans. of S.A. Phil. Soc., vol. xiv, pt. 4, 1903; vol. xvi, pt. 2, 1905.
6. MEAD, D. W. Hydrology. McGraw-Hill, New York, 1919.
7. PLUMMER, F. E. "Aspects of Rainfall in the Western Cape Province," Univ. of Pretoria, Series I, No. 22, 1932.
8. Rainfall Normals, 1925, and subsequent Annual Reports of the Chief Meteorologist of the Union of South Africa.
9. SCHAFFERNAK, F. Hydrographie. Wien, Julius Springer, 1935.
10. SCHUMANN, T. E. W., and THOMPSON, W. R. "A Study of South African Rainfall, Secular Variation and Agricultural Aspects," Pret. Univ., Series I, No. 28, 1934.
11. TIPPETT, L. H. C. The Methods of Statistics. Williams & Norgate, Ltd., London, 1931.
12. ZON, R. Forests and Water in the Light of Scientific Investigation. Gvt. Ptg. Office, Washington, U.S.A., 1927.

SPARID FISHES FROM PORTUGUESE EAST AFRICA, WITH
A NOTE ON THE GENUS *GYMNOCRANIUS* KLUNZINGER.

By J. L. B. SMITH.

(With Plate L and three Text-figures.)

(Read September 20, 1939.)

A recent visit to Portuguese East Africa has revealed that area to be almost virgin ground to the ichthyologist. On practically every collecting trip there new species, or known species new to South Africa, were secured. In the markets appeared quite frequently large species hitherto unknown from Southern Africa, while some, rare even in Natal waters, proved to be exceedingly abundant there. Among others a new Sparid fish, described below, was obtained. The present work extends our knowledge of the distribution of Sparid fishes on the eastern coast of South Africa.

I wish to record my appreciation of the courtesy and cordial assistance received from the provincial and local authorities of Moçambique, and especially from the staff of the Alvarez da Castro Museum of Lourenço Marques.

Family SPARIDAE.

Argyrops spinifer (Forsk.).

Smith, Trans. Roy. Soc. S.A., 1938, vol. xxvi, p. 256.

This species is not infrequently encountered in Portuguese East African waters. Most specimens are half-grown, and are captured by lines at moderate depth.

Argyrops filamentosus (Valenciennes).

Smith, *ibid.*, p. 257.

It is remarkable that this Indian Ocean species was not known from our waters until 1935, when Fowler recorded a specimen from the Zululand coast. I now find it not uncommon on the coast of Portuguese East Africa, specimens 200-300 mm. in length being not infrequently taken by lines in 2-10 fathoms.

Examination of this recent material confirms my view that the species falls with *spinifer* (Forsk.) in *Argyrops* Swainson.

Pterogymnus lanarius (Cuv.).

Smith, *ibid.*, p. 258, fig. 12.

Very occasional specimens of this species are captured in Delagoa Bay. It is uncommon even in Natal, occurring chiefly farther south.

Chrysoblephus puniceus (G. & T.).

Smith, *ibid.*, p. 265, fig. 15.

This characteristic Natal fish is the most abundant large Sparid of Portuguese East Africa. It attains a much larger size than in Natal waters, specimens over 600 mm. in length being not uncommon, and as plentiful at Beira as off Delagoa Bay. In large adults the caudal lobes become more elongate, but the body shape does not alter much with growth. The characteristic line below the eye is constant in all stadia. The related *C. cristiceps* (Cuv.) was not found.

Chrysoblephus anglicus (G. & T.).

Smith, *ibid.*, p. 269, fig. 16.

This species, which is almost unknown south of Natal and is comparatively rare even in Natal waters, becomes more plentiful farther north and attains a large size. Specimens 800 mm. in length are not uncommon in Delagoa Bay and at Beira. The characteristic shape of the head does not alter with age.

Genus *Polyamblyodon* Norman.

Smith, *ibid.*, p. 288.

In his revision of the Sea Breams, Norman (Ann. S.A. Mus., 1935, vol. xxxii, p. 17) included *Pachymetopon gibbosum* Pellegrin in the synonymy of *Pachymetopon grande* Günther. In my revision of the Sparidae of South Africa (Trans. Roy. Soc. S.A., 1938, vol. xxvi, pp. 225-305) Norman's opinion was accepted, since Pellegrin's original description of *gibbosum* (Bull. Soc. Zool. France, 1914, vol. xxxix, p. 264) was then not available. A copy of that work has since been received. In view of Pellegrin's description (*loc. cit.*) Norman was rather venturesome in sinking *gibbosum* as a synonym of *grande* Günther, since it is clearly distinct. Norman's opinion caused Pellegrin to re-examine his single type (when he found, contrary to his original statement, that the preopercle flange was partly scaly) and to reassert (Bull. de l'Acad. Malg., 1935, vol. xviii, p. 145) the validity of *gibbosum*, which he placed in *Pachymetopon* Günther, grouping it with *aeneum* Gilchrist and Thompson, which species also has scales on the preopercle flange.

While collecting recently in Portuguese East Africa there was obtained a fish fairly common there related to the Sea Breams of South Africa, but clearly distinct from all the known species. Investigation revealed that it is strikingly similar to *gibbosum* Pellegrin, differing from the description of that species (and not very widely) in scale counts and in one or two other points. To make certain that those differences were valid, as I was unable to obtain Pellegrin's type for examination, I then wrote to Dr. Pellegrin giving

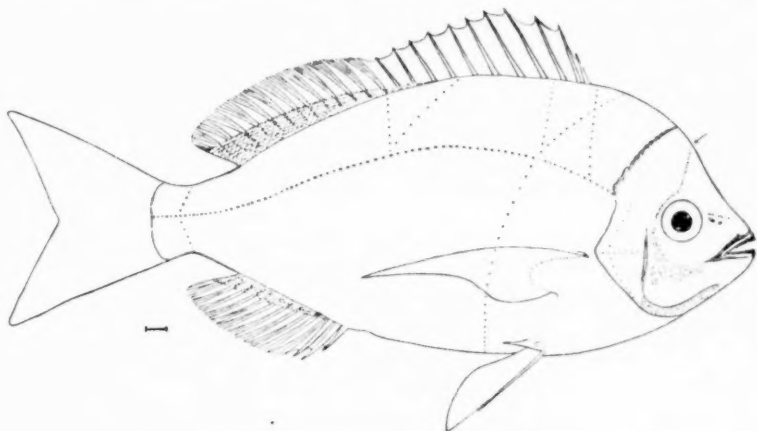


FIG. 1.—*Polyamblyodon cristiceps* sp. nov. (Type, 320 mm. length.)

The rows of dots show the number and disposition of the scale rows. The small arrow shows the anterior margin of the scaling on the head. The line represents 1 cm.

all details of my specimens, and requested him to re-examine his type with regard to them. His reply affirms the validity of his published description of *gibbosum*. Since the counts in my series of specimens are very uniform, I cannot but regard them as belonging to a new species, closely related to *gibbosum*, but distinguished from it as outlined below. *Gibbosum* and the new form, *cristiceps* sp. nov., are clearly congeneric and are generically distinct from all the known Sparid genera, save perhaps only the monotypic *Polyamblyodon* Norman, which is characterised (like *gibbosum* and *cristiceps*) by having a posterior band of molariform teeth in each jaw. The genotype, *Polyamblyodon germanus* (Barnard), has a fairly broad frontal region and naked preopercle flange, while the anterior incisors are large, chisel-like, and numerous. *P. gibbosum* and *cristiceps* have a sharp nape and some scales on the preopercle flange, while the incisors are rather small, lanceolate, and relatively few in number. If the latter two be accepted as congeneric with *germanus*, they form a definite subgroup within the genus. Their

close relationship, and the common difference from *germanus*, is as a compromise here given expression by subgeneric rank in *Polyamblyodon*.

The genus *Polyamblyodon* Norman may then be diagnosed as follows: Body ovate, compressed. Dorsal profile steep, and the supraoccipital elevated in the adult. Prefrontals well developed, forming a preorbital prominence. Preorbital fairly deep, the lower edge not notched. Posterior nostril slit-like. Cheek and opercular bones scaly, excepting preopercle flange, which is naked or partly scaly. Interorbital, snout, and chin naked. Dorsal with 11 moderate spines, not notched between spinous and soft portions. Soft dorsal and anal scaly on basal third of fin, no basal sheath. Scales feebly ctenoid. Lateral line tubes short, bifurcated posteriorly, with surface pores. Outer and anterior teeth incisiform, either chisel-like or lanceolate. An inner band of several rows of molariform teeth, either blunted or conical. Maxilla sometimes with an external roughened edge exposed beyond the lower preorbital margin. Gill-rakers lanceolate.

Key to the Species of Polyamblyodon.

- I. (*Polyamblyodon*) Nape broad. Outer teeth strong, chisel-like, extend round jaws. Preopercle flange naked *germanus*.
- II. (*Leptometopon*) Nape trenchant. Outer teeth rather slender, lanceolate, and present anteriorly only. A patch of scales on preopercle flange.
 - A. Lateral line 63. 19 gill-rakers *gibbosus*.
 - B. Lateral line 77-78. 16 gill-rakers *cristiceps*.

Subgenus *Leptometopon* nov.

Diagnosed in the key to the species (above).

Polyamblyodon (Leptometopon) cristiceps sp. nov.

Body oblong-ovate, fairly highly compressed, nape markedly cultrate. The dorsal profile of the head changes with age (text-fig. 2). In the young (260 mm.) the profile is moderately sloping, with a shallow gentle concavity above the anterior part of the eye. With age the profile becomes steeper and the concavity enlarges, until in a large adult the profile is almost sinuous, being strongly convex at the nuchal ridge, thence ventrally broadly concave to the somewhat simocephalous snout (text-fig. 2). The prefrontals are enlarged, forming a marked bulge on each side just anterior to the orbit and above the nostrils.

With age the lower jaw becomes increasingly more massive, until in large adults there is developed a strong "chin." Cheek and naked areas on head with large pores.

Depth 2.2-2.3, length of head 3.8-3.9 in length of body. Eye 3.6 (j.)-4.8 (ad.), snout 3.0-3.3, interorbital 2.6-3.1 (ad.), and postorbital part of

head 2.1 in length of head. Preopercle margin broadly concave, entire, angle enlarging somewhat with age. Outer edge of preopercle with radiate fine ridges. No opercular spine. Hind nostril slit-like or elongate-oval. Preorbital less than (1.3-1.2 in.) eye in juveniles, becomes deeper in adults, equal to eye. Pyloric caeca 4.

Mouth terminal, moderately protractile, maxilla extends to below the nostrils, not to eye. In juveniles the maxilla is largely concealed. The

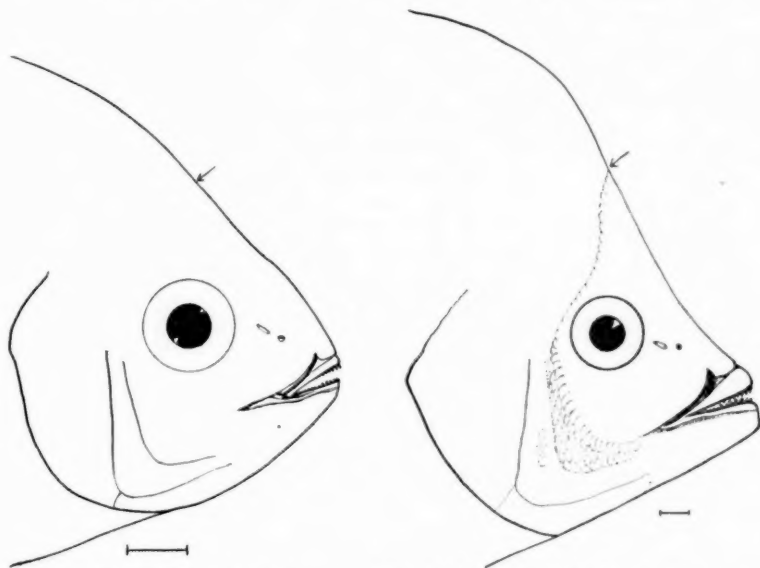


FIG. 2.—To show the change in shape of the head of *Polyamblyodon cristiceps* sp. nov. with growth. Left: of specimen 260 mm. in length. Right: specimen 510 mm. in length. Each line represents 1 cm. The small arrow shows the anterior margin of the scaling on the head. See fig. 1 for an intermediate stage.

maxilla has an external bony process along its anterior two-thirds, which is in the form of a downwardly projecting shelf. In juveniles the process is fairly small and thin, only the very sharp outer edge not being hidden below the lower preorbital margin when the mouth is closed. With age the process gradually increases and develops a thickened and rather rough outer lower margin, which is not covered by the preorbital. The anterior part of this ridge curls upwards round the anterior angle of the preorbital above the line of the upper jaw.

The dentition is in some respects close to that of *Gymnocrotaphus* Günther. In the front of each jaw is an external, almost exsert row of

moderate lanceolate incisiform teeth. Those in the lower jaw extend across the symphysis to half-way along the mandible, and are on each side discontinuous from an inner lateral row of similar but smaller teeth. The anterior teeth are lanceolate and but little compressed. With growth they change somewhat until in large adults the hinder teeth especially are almost



FIG. 3. — To show dentition in lower jaw of *Polyamblyodon cristiceps* sp. nov., semi-diagrammatic, from specimen 510 mm. in length. The line represents 1 cm. Inset, middle: a posterior molariform tooth. $\times 10$ approx.

conical and flare outwards. The inner lateral teeth are acutely triangular and incisiform. In the upper jaw there is also the outer anterior row and on each side an inner row, but there is not such an abrupt differentiation between them as in the lower jaw. The outer anterior teeth of the upper jaw are lanceolate and incisiform. In the upper jaw the outer series increases from 12 to 16, in the lower from 13 to 16 teeth with age. Inwards from, and behind, the outer series the inner posterior series increases from 12 to 15 incisiform sharp teeth on each side in each jaw, the anterior three being within the hinder of the front series. The total (outer) series of incisiform teeth increases from 30 to 40 in the upper, and from 31 to 40 in the lower jaw.

In each jaw immediately behind the incisors are small molariform teeth in a band, broadest anteriorly, tapering postero-laterally. These teeth are somewhat irregularly arranged in irregular rows in each jaw. The number of rows increases from 3 to 5 or 6 with age. The teeth are so close set as to form almost a pavement across the symphysis. In juveniles these teeth are partly rather blunt, partly with sharp-pointed apices. With age the inner teeth appear to become more typically conical and pointed above. In a large adult practically all have sharp apices (text-fig. 3). Palate and tongue edentate.

Sixteen gill-rakers on the lower limb of the anterior arch, of moderate size, 2.5 in gill-filaments, which are slightly greater than the eye diameter.

D XI, 13, first dorsal inserted just behind hind margin of opercle, scarcely notched between spinous and soft portions. Base of spinous dorsal 1.2 times, of soft dorsal 1.3 times head length. Spines moderate, fairly slender, membrane little incised. First spine 4.7, second 2.6-2.7, third 2.2-2.4, fourth and fifth subequal, longest 2.0-2.1 in length of head.

Remainder graduated shorter to the eleventh, which is 3.9-4.1 in head. First ray 3.0-3.1 in head, rays increase to third, 2.6 in head, thereafter subequal to the eleventh, last two shorter. Edge of soft fin gently and evenly convex.

A III, 10-11, inserted below the base of the fourth dorsal soft ray. First spine 4.6-4.8, second 3.2 in head, third equal or slightly longer. Soft rays about equal to the last spine, edge of fin gently and evenly convex. Base of anal 1.3 in head. Pectoral falcate, 1.35 times head, reaches to above anal origin. Ventrals 1.35 in head, inserted behind pectorals, below the base of the third or fourth dorsal spine. Axillary scale about one-third the length of the fin. Caudal moderately forked. Peduncle fairly slender, least depth 4.0-4.1 in depth of body.

Scales ctenoid, moderately small. Circuli fine, radiating striae fairly numerous. Exposed area of scale largely covered by adjacent radiating series of rather broad overlapping spinelets, forming a rough surface of characteristic appearance (see Plate L). Scales below the lateral line rather larger than those above. Lateral line scales of moderate size, tubes fairly wide, bifurcated posteriorly, with a series of pores along the line of each diverging tubule. In Plate L the chromatophores in the skin covering the scales are clearly visible.

L.l. 77-78, l.tr. $\frac{11-12}{22-24}$, 5-6 series on cheek. Scaling on nape extends to above centre of eye. Front part of head, *i.e.* interorbital, supraorbital, snout, most of cheek, and chin, naked. Preopercle flange mostly naked, but a small patch of scales in the middle of the wide flange near the angle (one small specimen shows no sign of scales on the preopercle flange). A row of heavy dark scales from suprascapula to occiput. Soft dorsal and anal densely scaly at base, deeper posteriorly. Pectoral base and most of caudal scaly.

Colour.—Uniform grey-blue to dusky above, shading to light below. Iris bronzy. Tips of ventrals, pectoral axil, and caudal lobes dark. Fins otherwise generally light.

Length.—Up to 560 mm.

Locality.—Delagoa Bay up to 20 fathoms, generally taken on lines.

Type.—An adult female, 320 mm. in length, in the Albany Museum.

This species is distinguished from *gibbosus* Pellegrin by the following characters:—

	<i>gibbosus</i> .	<i>cristiceps</i> .
Scales, lateral line	63	77-78
Scales, l.tr.	8/18	11/22
Gill-rakers	19	16
Length of pectoral, times head	1.5	1.35
Dorsal formula	XI, 12	XI, 13
Outer incisors	27/24	12-15/12-15

P. cristiceps is not a very plentiful species in Mozambique waters, nor has it any well-known common name. It is not very highly esteemed as a table fish.

Of seven specimens examined, all were females, none fully ripe (August).

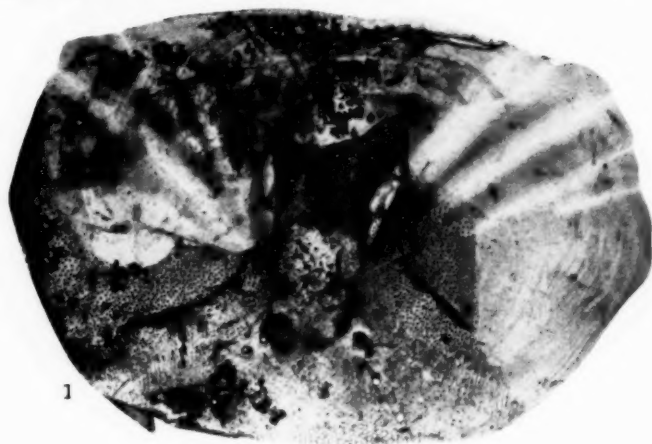
Genus *Gymnocranius* Klunzinger.

In a revision of the Sparid and Denticid fishes of South Africa (Smith, Trans. Roy. Soc. S.A., 1938, vol. xxvi, p. 225) previous workers were followed in accepting *Gymnocranius* as a Denticid genus, since superficially it appears to belong there, and the only specimens available to me were loaned, and not for dissection. Preliminary superficial dissection of material recently obtained in Portuguese East Africa has shown that by the nature of the maxillary bones *Gymnocranius* cannot belong either to the SPARIDAE or to the DENTICIDAE. In so far as my present examination has proceeded, *Gymnocranius* appears almost certainly to fall in the LUTIANIDAE, but a special study of the genus is in progress.

Hitherto only the species *Gymnocranius robinsoni* (Gilchrist and Thompson) has been recorded from the South African region. *G. griseus* (Schlegel) has now been found to be fairly abundant in Delagoa Bay. This species has been recorded from Mauritius to Japan.

I wish to express my gratitude to the National Research Board for financial assistance.

ALBANY MUSEUM,
GRAHAMSTOWN,
2nd September 1939.



1



2

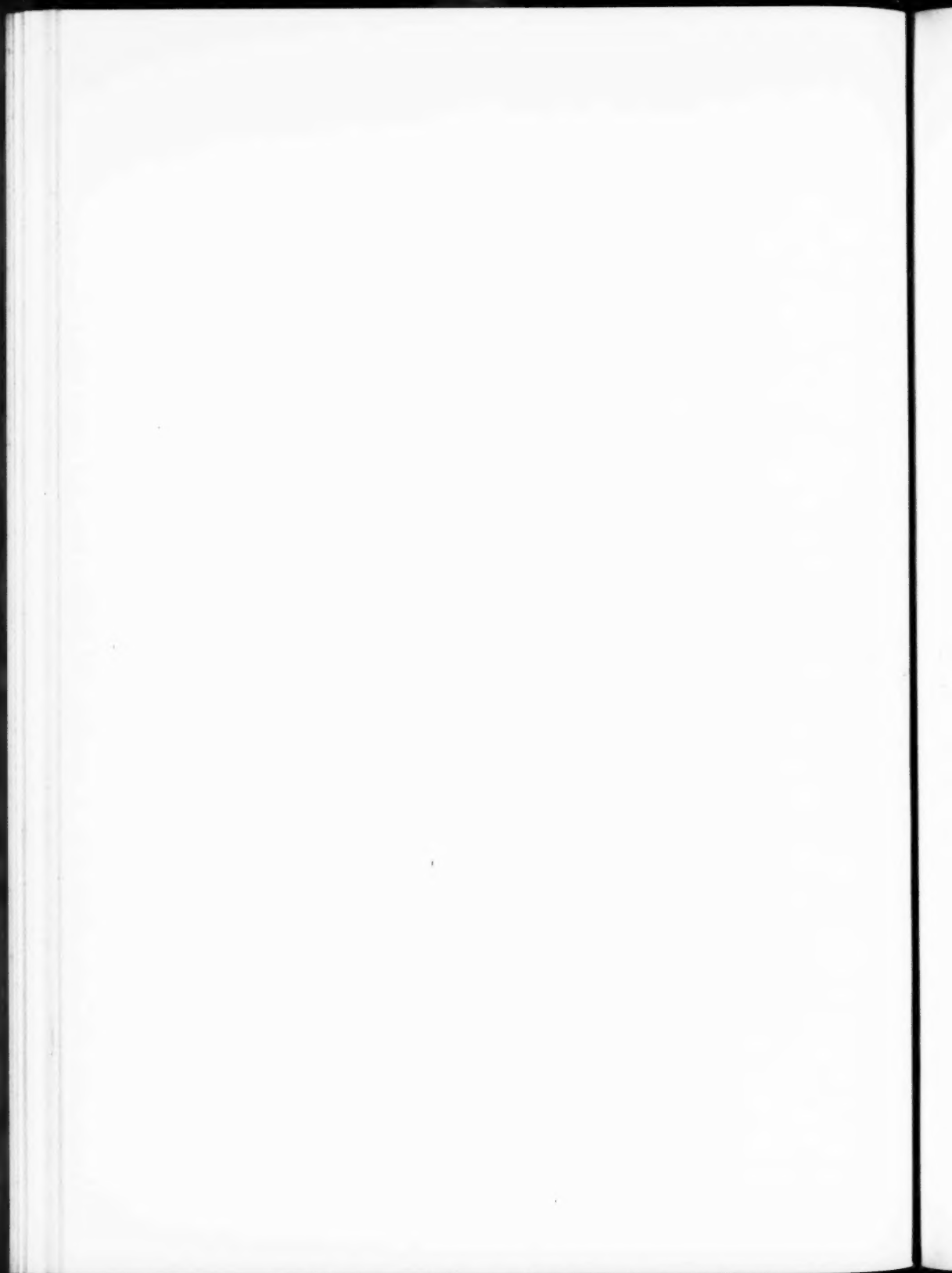


3

Polyamblyodon cristicps sp. nov. Scales.

1. 11th lateral line scale. $\times 12$.
2. The 7th scale ventral from the 11th lateral line scale. $\times 5.5$.
3. The 4th scale dorsal from the 11th lateral line scale. $\times 8$.

The posterior margin of each scale below.



ORIENTABLE MANIFOLDS CONSTRUCTED FROM A SOLID CUBE.

By D. B. SUMNER.

(Communicated by A. BROWN.)

(Read August 16, 1939.)

1. H. Kneser* and M. Kreines† have given accounts of the formation of Poincaré Spaces from solid 3-dimensional figures in Euclidian R^3 . In general their method is to identify in pairs the faces of such a solid figure (in the first case a dodekahedron, and in the second a sphere); in both cases it is shown that the resulting complex is an orientable manifold with the Betti numbers of a 3-sphere, but that, the Fundamental Group being different from that of the 3-sphere, it is not the homoeomorph of the 3-sphere.

The method used by Kneser and Kreines will be used to obtain all possible orientable manifolds from a solid cube, whether those manifolds be Poincaré spaces or not.

A brief account of some of the terms used in this paper is given in the Appendix.

2. There is a wide range of possibility in pairing off and identifying the faces of the solid cube C . The procedure adopted will, however, be governed by the theorem: ‡ the complex formed by identifying in pairs the faces of a solid polyhedron is a manifold if, and only if, its characteristic is zero.

Before examining all possibilities, some definitions and preliminary results will be given.

3. *Orientability*.—If the complexes to be formed from C are to be orientable, it is necessary (and sufficient) that in each pair of faces to be identified, opposed orientations should be induced. In practice this means that if the orientation of one member of the pair is clockwise, that of the other member will have to be counter-clockwise, as it would seem to an observer from outside C .

4. *Definitions*.—(1) The terms "clockwise" and "counter-clockwise" are to be taken with reference to an observer outside C , as in paragraph 3.

* Jhber. Deutsch. Math. Vereinig., 38 (1929), pp. 248-260.

† Rend. del Circolo Mat. di Palermo, Ivi (1932), pp. 277-280.

‡ See Seifert and Threlfall, *Topologie*, p. 208.

- (2) Opposite faces of C will be opposite in the usual sense of the word.
- (3) Adjacent faces of C will be faces which have an edge in common.
- (4) Rotation of a face through an angle will mean rotation in its plane in a clockwise direction about its central point.

(5) Identification: when one face of any pair has been rotated through some multiple of $\pi/2$, it will be identified with its other member by mapping on one another mirror-images with respect to

- (a) a plane equidistant from the two members in the case of a pair of opposite faces;
- (b) the common edge, in the case of a pair of adjacent faces.

The relation between the two members is clearly topological. Vertices are identified with vertices, edges with edges, and the condition of paragraph 3 is satisfied.

(6) For convenience, one member of a pair of opposite faces will be designated as the "upper," and the other as the "lower." These terms refer to no intrinsic properties of C , and it is clear that the same effect is produced on C if the rotation which precedes identification is performed on the upper or the lower member of any pair.

(7) In the same manner, one member of a pair of adjacent faces will be designated as the "right-hand," and the other as the "left-hand" member. The remark in (6) also applies to these two terms.

(8) By "complementary space" of C will be meant the closure of the complement $R^3 - C$ in Euclidian R^3 . The term will have an analogous meaning for any complex constructed from C by means of rotations and identifications.

5. *Pairing of Faces.*—The faces of C may be paired in the following ways:—

- (1) Every pair may consist of opposite faces;
- (2) One pair may consist of opposite faces, and the remaining two of adjacent faces;
- (3) Every pair may consist of adjacent faces.

6. *Identification in Pairs of Faces.*—There are four ways of identifying faces in any one pair, whether of opposite or adjacent faces. For opposite faces the upper face, and for adjacent faces the right-hand face, may first be rotated through any one of the angles $\pi/2$, π , $3\pi/2$, or 2π , before the two faces are identified with one another in the manner described in paragraph 4. Vertices are identified with vertices, and edges with edges.

7. *Theorem A.*—Two closed complexes K_1^3 and K_2^3 , formed by pairing off and identifying faces of two solid polyhedra P_1 and P_2 , are homoeomorphic if, and only if, K_1^2 and K_2^2 , the complexes arising from the boundaries P_1 and P_2 after identification of the faces, are homoeomorphic.

For if \mathbb{K}_1^3 and \mathbb{K}_2^3 are homoeomorphic, then \mathbb{K}_1^2 and \mathbb{K}_2^2 are homoeomorphic.

Conversely, let \mathbb{K}_1^3 and \mathbb{K}_2^3 be formed from P_1 and P_2 in the manner described; and let \mathbb{K}_1^2 and \mathbb{K}_2^2 be homoeomorphic. It is required to prove the existence of a topological mapping F of \mathbb{K}_1^3 on \mathbb{K}_2^3 . There exists a topological mapping f , such that $f(\mathbb{K}_1^2) = \mathbb{K}_2^2$. Let x_0 be a fixed interior point of \mathbb{K}_1^3 , and y_0 a fixed interior point of \mathbb{K}_2^3 . Let x_0 be joined to any point t of \mathbb{K}_1^2 , and y_0 to the image point $f(t)$ of \mathbb{K}_2^2 . Also let $r_t(x) = d(x, t)$, where x is any interior point of \mathbb{K}_1^3 , and the distance $d(x, t)$ exists. Similarly, let y be any interior point of \mathbb{K}_2^3 , and $s_t(y) = d[y, f(t)]$. Then let the point x be mapped on the point y in such a way that

$$r_t(x)/r_t(x_0) = s_t(y)/s_t(y_0). \quad F$$

Clearly, this mapping F is topological, and under it the interior of \mathbb{K}_1^3 is mapped on the interior of \mathbb{K}_2^3 ; moreover, when $x = t$, $y = f(t)$. So that F is a topological mapping of \mathbb{K}_1^3 on \mathbb{K}_2^3 .

Theorem B.—The complementary space of any complex \mathbb{K}^3 constructed in the manner described above, is the homoeomorph of that complex.

For the exterior $[R^3 - \mathbb{K}^3]$ may be topologically mapped on the interior of \mathbb{K}^3 by an inversion with respect to the boundary complex. The boundary complex is common to both the complex and its complementary space. Theorem A may then be applied.

8. *Orientable Manifolds formed from Three Pairs of Opposite Faces:*—As the upper member of any pair of opposite faces may before identification be rotated through any one of the four angles $\pi/2$, π , $3\pi/2$, 2π , there will arise the following sets of possibilities:—

A: (α, α, α) ,

B: (α, α, β) ,

C: (α, β, γ) ,

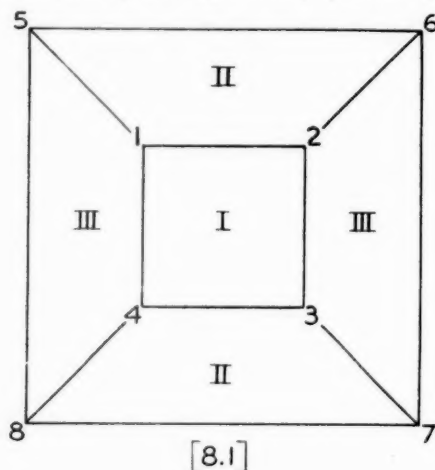
where the angles α, β, γ range over $\pi/2$, π , $3\pi/2$, and 2π , and $\alpha \neq \beta \neq \gamma$.

For an orientable 3-manifold $*p^0 = p^3 = 1$, $p^1 = p^2$; and the Fundamental Group will be that of the boundary complex after identification.† Thus all the Homology properties and the Fundamental Group may be derived by considering the “mesh” of the boundary complex, this mesh being obtained by a stereographic projection of the surface of the polyhedron on the euclidian plane.

8A. The method of obtaining the mesh for the case $(\frac{\pi}{2}, \frac{\pi}{2}, \frac{\pi}{2})$ will be worked out in detail as an illustration of the method used for the remaining cases in paragraph 8. The diagram (8.1) represents the edges of the

* Seifert and Threlfall, p. 205.

† *Ibid.*, p. 214.



cube C. The faces to be identified are denoted by the same Roman numeral. Applying $(\pi/2)$ to the faces I, we obtain

$$\begin{array}{llll} 1 \equiv 6, & 4 \equiv 5, & 3 \equiv 8, & 2 \equiv 7, \\ \vec{41} \equiv \vec{56}, & \vec{34} \equiv \vec{85}, & \vec{23} \equiv \vec{78}, & \vec{12} \equiv \vec{67}. \end{array}$$

Now, applying the operation $(\pi/2)$ to the faces II, we have

$$\begin{array}{llll} 1 \equiv 8, & 2 \equiv 4, & 6 \equiv 3, & 5 \equiv 7, \\ \vec{15} \equiv \vec{87}, & \vec{21} \equiv \vec{48}, & \vec{62} \equiv \vec{34}, & \vec{56} \equiv \vec{73}. \end{array}$$

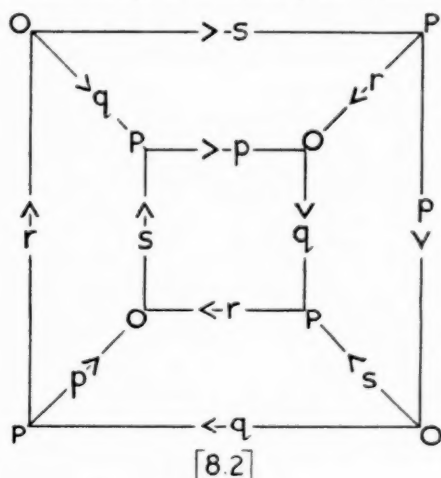
Finally, applying the operation $(\pi/2)$ to the faces III:—

$$\begin{array}{llll} 2 \equiv 5, & 6 \equiv 8, & 7 \equiv 4, & 3 \equiv 1, \\ \vec{26} \equiv \vec{58}, & \vec{67} \equiv \vec{84}, & \vec{73} \equiv \vec{41}, & \vec{32} \equiv \vec{15}. \end{array}$$

All these results may be embodied in diagram (8.2). We thus obtain two distinct vertices O and P; and four distinct edges p, q, r and s . Accordingly the characteristic $N = -2 + 4 - 3 + 1 = 0$, so that the complex we have constructed is a manifold. We then have

$$H^1 = \begin{array}{c|ccc} & \text{I} & \text{II} & \text{III} \\ \hline p & 1 & 1 & 1 \\ q & 1 & 1 & -1 \\ r & 1 & -1 & -1 \\ s & 1 & -1 & 1 \end{array} \quad \text{i.e.} \quad \begin{pmatrix} 2 & 0 & 0 \\ 0 & 2 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}; \quad H^2 = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix};$$

$$\text{and } p^2 = a^2 - \gamma^2 - \gamma^1 = 3 - 0 - 3 = 0 = p^1.$$



Also, for the Fundamental Group we have the relations

$$\begin{aligned} pqr s &= 1, \\ r q s^{-1} p^{-1} &= 1, \\ q p r^{-1} s^{-1} &= 1. \end{aligned}$$

Results for the remaining cases will be summarised briefly:

(π, π, π) : a manifold because $N = -4 + 6 - 3 + 1 = 0$.

1-torsions = 2; $p^2 = p^1 = 0$.

$$\begin{aligned} \mathfrak{J}: \quad pqr s &= 1, \\ urt^{-1} p^{-1} &= 1, \\ tsuq^{-1} &= 1. \end{aligned}$$

$(3\pi/2, 3\pi/2, 3\pi/2)$: this complex is the complementary space of $(\frac{\pi}{2}, \frac{\pi}{2}, \pi/2)$; it is therefore a manifold and its properties have been dealt with.

$(2\pi, 2\pi, 2\pi)$: a manifold because $N = -1 + 3 - 3 + 1 = 0$.

No 1-torsions; $p^2 = p^1 = 3$.

$$\begin{aligned} \mathfrak{J}: \quad sps^{-1} p^{-1} &= 1, \\ sqs^{-1} q^{-1} &= 1, \\ pqp^{-1} q^{-1} &= 1. \end{aligned}$$

It is the topological product of three circles.

8B. $(\pi/2, \pi/2, \pi)$; $(\pi/2, \pi/2, 3\pi/2)$; $(\pi/2, \pi/2, 2\pi)$; $(\pi, \pi, \pi/2)$:

VOL. XXVIII, PART II.

For none of these cases is the characteristic equal to zero, so that none is a manifold. The following are their respective complementary spaces:—

$(3\pi/2, 3\pi/2, \pi)$, $(3\pi/2, 3\pi/2, \pi/2)$, $(3\pi/2, 3\pi/2, 2\pi)$, $(\pi, \pi, 3\pi/2)$; they therefore do not form manifolds.

$(\pi, \pi, 2\pi)$: a manifold because $N = -2 + 4 - 3 + 1 = 0$.

1-torsions = 2, 2; $p^2 = p^1 = 0$.

$$\begin{aligned}\mathfrak{J}: \quad pqrq^{-1} &= 1, \\ p s r^{-1} s^{-1} &= 1, \\ (q s^{-1})^2 &= 1.\end{aligned}$$

$(2\pi, 2\pi, \pi/2)$: a manifold because $N = -1 + 3 - 3 + 1 = 0$.

1-torsions = 2; $p^2 = p^1 = 1$.

$$\begin{aligned}\mathfrak{J}: \quad pqp^{-1}r &= 1, \\ qpr^{-1}p^{-1} &= 1, \\ qrq^{-1}r^{-1} &= 1.\end{aligned}$$

$(2\pi, 2\pi, \pi)$: a manifold because $N = -1 + 3 - 3 + 1 = 0$.

1-torsions = 2, 2; $p^2 = p^1 = 1$.

$$\begin{aligned}\mathfrak{J}: \quad pqp^{-1}q &= 1, \\ prp^{-1}r &= 1, \\ qrq^{-1}r^{-1} &= 1.\end{aligned}$$

$(2\pi, 2\pi, 3\pi/2)$: this is the complementary space, and therefore the homoeomorph of $(2\pi, 2\pi, \pi/2)$.

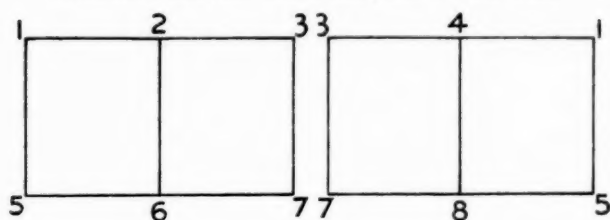
8c. It is easily verified that for none of the complexes (α, β, γ) is the characteristic zero; so that none of these cases gives rise to a manifold.

9. *Manifolds formed from Two Pairs of Adjacent and One Pair of Opposite Faces.*—The following possibilities arise:—

$$\begin{aligned}(A): \quad (\alpha\alpha; \gamma), \\ (B): \quad (\alpha\beta; \gamma),\end{aligned}$$

where α, β, γ have the values $\pi/2, \pi, 3\pi/2$, and 2π , and $\alpha \neq \beta$. The first two symbols in the brackets will denote operations on the pairs of adjacent faces; and the last symbol operations on the pair of opposite faces. It is immediately obvious that $\alpha\beta$ will have the same effect on the edges, faces and vertices of C as $\beta\alpha$.

For these cases we shall use a modification of the previous diagrams. The two pairs of adjacent faces will be represented by the diagram (9.1). The upper and lower members of the pair of opposite faces will be 1234 and 5678. It will be clear from the manner of using these figures that there is no need to indicate the upper and lower faces in any greater detail.



[9.1]

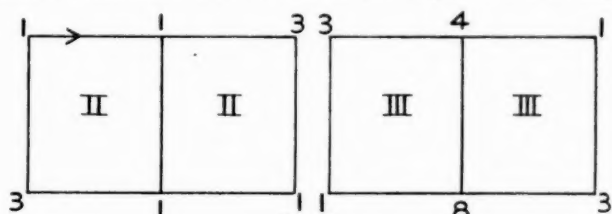
9A. We shall illustrate the method for the case $(\pi/2, \pi/2, r\pi/2)$, $r=1, 2, 3, 4$. Applying $(\pi/2)$ to the adjacent pair II, we get

$$\begin{aligned} 6 \equiv 2 \equiv 7 \equiv 1, \quad 3 \equiv 5, \\ \vec{76} \equiv \vec{62} \equiv \vec{21}, \quad \vec{23} \equiv \vec{15}, \quad \vec{37} \equiv \vec{56}; \end{aligned}$$

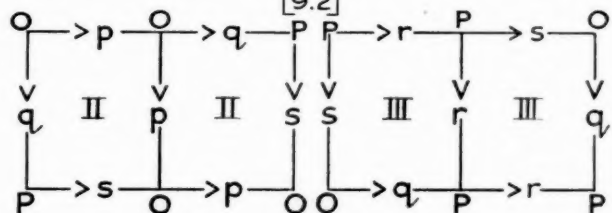
and applying $(\pi/2)$ to the pair III, we have

$$\begin{aligned} 3 \equiv 4 \equiv 8 \equiv 5, \quad 1 \equiv 7, \\ \vec{58} \equiv \vec{84} \equiv \vec{43}, \quad \vec{41} \equiv \vec{37}, \quad \vec{15} \equiv \vec{78}. \end{aligned}$$

These operations are indicated in diagrams (9.2), (9.3), where for convenience letters are used to denote the edges. At this stage (i.e.



[9.2]



[9.3]

before any operation $r\pi/2$ has been applied to the pair of opposite faces), there are two vertices and four edges. Now the operations $r\pi/2$ are applied to the pair of opposite faces.

$\pi/2$: $p=r$; $q=s$; $O=P$; $N = -1+2-3+1 \neq 0$, so that this complex is no manifold.

π : $p=q=r=s$; $O=P$; $N = -1+1-3+1 \neq 0$, not a manifold.

2π : $p=s=r=q$; $O=P$; $N = -1+1-3+1 \neq 0$, not a manifold.

$3\pi/2$: $p=p$, $q=q$, $r=r$, $s=s$; $O \neq P$; a manifold because

$$N = -2+4-3+1=0.$$

For this manifold:—

$$\begin{array}{c} \text{I} \quad \text{II} \quad \text{III} \\ H^1 = p \begin{array}{|c|c|c|} \hline 1 & 2 & 0 \\ \hline \end{array} \quad \text{i.e.} \quad \begin{pmatrix} 8 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}; \quad H^2 = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \\ q \begin{array}{|c|c|c|} \hline 1 & -1 & -1 \\ \hline \end{array} \\ r \begin{array}{|c|c|c|} \hline 1 & 0 & 2 \\ \hline \end{array} \\ s \begin{array}{|c|c|c|} \hline 1 & -1 & -1 \\ \hline \end{array} \end{array}$$

$$p^2 = a^2 - \gamma^2 - \gamma^1 = 3 - 0 - 3 = 0 = p^1;$$

$$\mathfrak{J}: \quad pqr s = 1,$$

$$p^2 s^{-1} q^{-1} = 1,$$

$$s^{-1} r^2 q^{-1} = 1.$$

The remaining possibilities under 8A will be summarised below.

$(\pi\pi; \pi/2)$: a manifold because $N=0$; 1-torsions = 4; $p^2=0=p^1$.

$$\mathfrak{J}: \quad pqp s = 1,$$

$$ptq^{-1}t = 1,$$

$$pts^{-1}t = 1.$$

$(\pi\pi, \pi)$, a manifold because $N=0$; 1-torsions = 4, 4; $p^2=0=p^1$.

$$\mathfrak{J}: \quad p^2 q^2 = 1,$$

$$ptq^{-1}t = 1,$$

$$qt p^{-1}t = 1.$$

$(\pi\pi, 3\pi/2)$: the complementary space of $(\pi\pi, \pi/2)$, and therefore its homoeomorph.

$(\pi\pi, 2\pi)$: a manifold because $N=0$; 1-torsions = 2, 2; $p^2=1=p^1$.

$$\mathfrak{J}: \quad p^2 r^2 = 1,$$

$$pt p^{-1}t = 1,$$

$$rt r^{-1}t = 1.$$

This manifold is not a Poincaré Space.

$\left(\frac{3\pi}{2} \frac{3\pi}{2}; \pi\right)$, $\left(\frac{3\pi}{2} \frac{3\pi}{2}; \frac{3\pi}{2}\right)$, $\left(\frac{3\pi}{2} \frac{3\pi}{2}; 2\pi\right)$ are the complementary spaces of $(\pi/2\pi/2; \pi)$, $(\pi/2\pi/2; \pi/2)$, $(\pi/2\pi/2; 2\pi)$ respectively, complexes which have already been shown not to be manifolds.

$\left(\frac{3\pi}{2}, \frac{3\pi}{2}; \frac{\pi}{2}\right)$: this is the complementary space of $\left(\frac{\pi}{2}, \frac{\pi}{2}; \frac{3\pi}{2}\right)$, which has already been dealt with.

$(2\pi 2\pi; \pi/2)$: a manifold because $N=0$; 1-torsions, none; $p^2=p^1=1$.

$$\begin{aligned}\mathfrak{J}: \quad p s p r^{-1} &= 1, \\ p t p r^{-1} &= 1.\end{aligned}$$

$(2\pi 2\pi; \pi)$: a manifold because $N=0$; no 1-torsions; $p^2=p^1=1$.

$$\begin{aligned}\mathfrak{J}: \quad p s q^{-1} r^{-1} &= 1, \\ q t p^{-1} r^{-1} &= 1.\end{aligned}$$

$(2\pi 2\pi; 3\pi/2)$: this complex is the complementary space, and therefore the homoeomorph of $(2\pi 2\pi; \pi/2)$, which has already been dealt with.

$(2\pi 2\pi; 2\pi)$: a manifold because $N=0$; no 1-torsions; $p^2=p^1=1$.

$$\begin{aligned}\mathfrak{J}: \quad p s p^{-1} r^{-1} &= 1, \\ u t u^{-1} r^{-1} &= 1.\end{aligned}$$

9B. The technique for this type being no different than for 9A, the results will be summarised briefly without illustration.

$(\pi/2\pi; \pi/2)$: a manifold because $N = -1 + 3 - 3 + 1 = 0$; 1-torsions = 4; $p^2=p^1=0$.

$$\begin{aligned}\mathfrak{J}: \quad r p^{-1} s p^{-1} &= 1, \\ p^2 s^2 &= 1, \\ s r s p &= 1.\end{aligned}$$

$(\pi/2\pi; 3\pi/2)$: a manifold because $N=0$; 1-torsions = 12; $p^2=p^1=0$;

$$\begin{aligned}\mathfrak{J}: \quad p^2 r^2 &= 1, \\ r q^{-1} r p^{-1} &= 1, \\ r^3 q &= 1.\end{aligned}$$

$(\pi/2\pi; \pi)$ and $(\pi/2\pi; 2\pi)$: not manifolds as $N \neq 0$.

$\left(\frac{\pi}{2}, \frac{3\pi}{2}; \frac{r\pi}{2}\right)$: $N \neq 0$ for all r , so that none of these forms a manifold.

$(\pi/2\pi; \pi/2)$: a manifold because $N=0$; 1-torsions = 4; $p^2=p^1=0$.

$$\begin{aligned}\mathfrak{J}: \quad p q &= 1, \\ p^2 q^{-2} &= 1, \\ t p^{-1} q p^{-1} &= 1.\end{aligned}$$

$(\pi/2\pi; 3\pi/2)$: a manifold because $N=0$; 1-torsions = 4; $p^2=p^1=0$.

$$\begin{aligned} \mathfrak{J}: \quad & pq = 1, \\ & p^2 q^{-2} = 1, \\ & q^3 t = 1. \end{aligned}$$

$(\pi/2 \ 2\pi; \ \pi)$ and $(\pi/2 \ 2\pi; \ 2\pi)$: not manifolds, as $N \neq 0$.

$\left(\frac{3\pi}{2}; \ \pi/2\right)$: this complex is the complementary space, and therefore the homoeomorph of the manifold $(\pi/2\pi; \ 3\pi/2)$.

$\left(\frac{3\pi}{2}; \ \frac{3\pi}{2}\right)$: the complementary space and therefore the homoeomorph of $(\pi/2\pi; \ \pi/2)$.

$(\pi 2\pi; \ \pi/2)$: a manifold because $N = -2 + 4 - 3 + 1 = 0$; 1-torsions = 2; $p^2 = p^1 = 0$.

$$\begin{aligned} \mathfrak{J}: \quad & pq = 1, \\ & ptq^{-1}t = 1, \\ & uplp = 1. \end{aligned}$$

$(\pi 2\pi; \ \pi)$: a manifold because $N = -1 + 3 - 3 + 1 = 0$; 1-torsions = 2; $p^2 = p^1 = 1$;

$$\begin{aligned} \mathfrak{J}: \quad & (pt)^2 = 1, \\ & pu^{-1}pt^{-1} = 1. \end{aligned}$$

$(\pi 2\pi; \ 3\pi/2)$: the complementary space, and therefore the homoeomorph of $(\pi 2\pi; \ \pi/2)$.

$(\pi 2\pi; \ 2\pi)$: a manifold because $N = -2 + 4 - 3 + 1 = 0$; 1-torsions = 2, 2; $p^2 = p^1 = 0$.

$$\begin{aligned} \mathfrak{J}: \quad & p^2 = 1, \\ & ptp^{-1}t = 1, \\ & trur^{-1} = 1. \end{aligned}$$

$\left(\frac{3\pi}{2} 2\pi; \ \pi\right)$ and $\left(\frac{3\pi}{2} 2\pi; \ 2\pi\right)$: as $N \neq 0$, these are not manifolds.

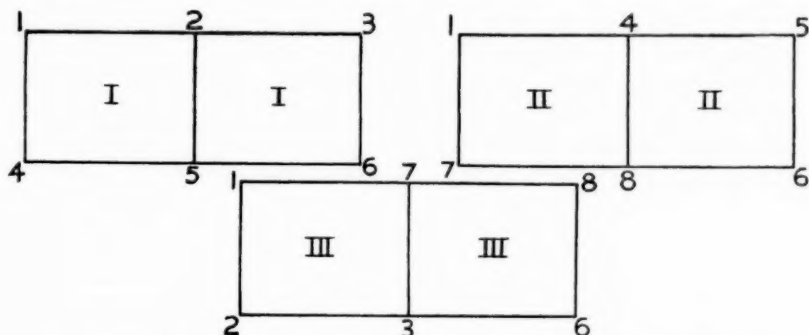
$\left(\frac{3\pi}{2} 2\pi; \ \frac{\pi}{2}\right)$: the complementary space, and therefore the homoeomorph of $(\pi/2 \ 2\pi; \ 3\pi/2)$.

$\left(\frac{3\pi}{2} 2\pi; \ \frac{3\pi}{2}\right)$: the complementary space, and therefore the homoeomorph of $(\pi/2 \ 2\pi; \ \pi/2)$.

$(\pi 3\pi/2; \ \pi)$ and $(\pi 3\pi/2; \ 2\pi)$ are the complementary spaces and therefore the homoeomorphs of $(\pi/2\pi; \ \pi)$ and $(\pi/2\pi; \ 2\pi)$ respectively.

10. *Complexes formed from Three Pairs of Adjacent Faces.*—In order to examine whether complexes formed from this manner of pairing the faces

of C are manifolds, we represent the three pairs of adjacent faces in plan, as in diagram (10), marking in which vertices, and which edges are the same.



Before identifying we may first, in each pair, rotate the right-hand member through an angle $r\pi/2$, $r=1, 2, 3$ and 4 . The cases which will arise are therefore:—

$$A: (a, a, a),$$

$$B: (a, a, \beta),$$

$$C: (a, \beta, \gamma),$$

where $a, \beta, \gamma = r\pi/2$, $r=1, 2, 3$ and 4 , and $a \neq \beta \neq \gamma$.

10A. The case $(\pi/2, \pi/2, \pi/2)$ will be worked out in detail as an illustration of the method. When the operation $(\pi/2)$ is performed on the pair I (diagram 10), we have:—

$$\begin{aligned} \vec{12} \equiv \vec{25} \equiv \vec{56}, \quad \vec{23} \equiv \vec{14}, \quad \vec{36} \equiv \vec{45}, \\ 1 \equiv 2 \equiv 5 \equiv 6, \quad 3 \equiv 4. \end{aligned}$$

The same operation on the pair II gives:—

$$\begin{aligned} \vec{14} \equiv \vec{48} \equiv \vec{86}, \quad \vec{45} \equiv \vec{17}, \quad \vec{56} \equiv \vec{78}, \\ 1 \equiv 4 \equiv 8 \equiv 6, \quad 5 \equiv 7. \end{aligned}$$

And from the same operation on the pair III:—

$$\begin{aligned} \vec{17} \equiv \vec{73} \equiv \vec{36}, \quad \vec{78} \equiv \vec{12}, \quad \vec{86} \equiv \vec{23}, \\ 1 \equiv 7 \equiv 3 \equiv 6, \quad 8 \equiv 2. \end{aligned}$$

Combining all these results, we find that the operations $(\pi/2, \pi/2, \pi/2)$ on C give:—

$$\begin{aligned} 1 \equiv 2 \equiv 3 \equiv 4 \equiv 5 \equiv 6 \equiv 7 \equiv 8 \equiv P, \text{ say;} \\ \vec{12} \equiv \vec{25} \equiv \vec{56} \equiv \vec{78}; \quad \vec{23} \equiv \vec{14} \equiv \vec{48} \equiv \vec{86}; \quad \vec{36} \equiv \vec{45} \equiv \vec{17} \equiv \vec{73}. \end{aligned}$$

Thus we have in the end one vertex P, and three edges $\vec{12}$, $\vec{23}$, $\vec{36}$, which, for convenience we shall denote by p , q and r respectively. Accordingly $N = -1 + 3 - 3 + 1 = 0$, and the complex is therefore a manifold. For this manifold:—

$$H^1 = p \begin{array}{c|ccc} & \text{I} & \text{II} & \text{III} \\ \hline & 2 & -1 & -1 \\ q & -1 & 2 & -1 \\ r & -1 & 1 & 2 \end{array} \quad i.e. \quad \begin{pmatrix} 0 & 3 & 0 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{pmatrix}; \quad H^2 = \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$$

$$p^2 = a^2 - \gamma^2 - \gamma^1 = 3 - 0 - 2 = 1 = p^1;$$

$$\mathfrak{I}: \quad p^2 r^{-1} q^{-1} = 1,$$

$$q^2 p^{-1} r^{-1} = 1,$$

$$r^2 q^{-1} p^{-1} = 1.$$

The remaining cases of paragraph 10A are summarised below:—

(π, π, π) : not a manifold because $N = -2 + 3 - 3 + 1 \neq 0$.

$(3\pi/2, 3\pi/2, 3\pi/2)$: the complementary space, and therefore the homoeomorph of $(\pi/2, \pi/2, \pi/2)$.

$(2\pi, 2\pi, 2\pi)$: a manifold because $N = -2 + 4 - 3 + 1 = 0$; no 1-torsions;

$$p^2 = p^1 = 0;$$

$$\mathfrak{I}: \quad pu = pa = px = 1.$$

10B. As the method for these cases is no different from that for paragraph 10A, results will be summarised:—

$(\pi/2, \pi/2, \pi)$; $(\pi/2, \pi/2, 3\pi/2)$; $(\pi/2, \pi/2, 2\pi)$; $(\pi, \pi, \pi/2)$; $(\pi, \pi, 3\pi/2)$; $(\pi, \pi, 2\pi)$; in none of these cases is the characteristic zero, so that none is a manifold.

$(3\pi/2, 3\pi/2, \pi/2)$, $(3\pi/2, 3\pi/2, \pi)$, $(3\pi/2, 3\pi/2, 2\pi)$ are the complementary spaces of $(\pi/2, \pi/2, 3\pi/2)$, $(\pi/2, \pi/2, \pi)$, and $(\pi/2, \pi/2, 2\pi)$ respectively, and are therefore not manifolds.

$(2\pi, 2\pi, \pi/2)$: a manifold because $N = -2 + 4 - 3 + 1 = 0$; 1-torsions = 2;
 $p^2 = p^1 = 0$;

$$\mathfrak{I}: \quad pu = p^{-1}x = t^2 = 1.$$

$(2\pi, 2\pi, \pi)$: a manifold because $N = -2 + 4 - 3 + 1 = 0$; no 1-torsions;
 $p^2 = p^1 = 0$;

$$\mathfrak{I}: \quad pu = px = pt = 1.$$

$(2\pi, 2\pi, 3\pi/2)$: the complementary space, and therefore the homoeomorph of $(2\pi, 2\pi, \pi/2)$.

10C. It is easily verified that for none of the complexes $(\pi/2, \pi, 3\pi/2)$, $(\pi/2, \pi, 2\pi)$, $(\pi/2, 3\pi/2, 2\pi)$, $(\pi, 3\pi/2, 2\pi)$ is the characteristic zero; so that none of these is a manifold.

11. The following facts emerge from the above investigation:—

- (i) not all possibilities in pairing and identifying the faces of C give rise to orientable manifolds;
- (ii) not all the possibilities which give rise to orientable manifolds give rise to topologically different ones;
- (iii) where topologically distinct orientable manifolds are obtained, they are distinguished from one another by
 - (a) having different Betti Numbers of dimension 1;
 - (b) or having different torsion numbers of dimension 1;
 - (c) or having non-isomorphic Fundamental Groups.

APPENDIX.

BETTI AND TORSION NUMBERS, EULER CHARACTERISTIC.

The k -simplexes of any complex K^n may be assembled in any arbitrary manner into k -chains, which form an abelian group. The k -cycles, i.e. the k -chains with zero boundary, form a subgroup of this group.

Homology classes of K^n for any dimension $k < n$, are defined by placing in one class all k -cycles which are homologous to one another. These homology classes also form a group, the k^{th} homology group \mathfrak{H}^k of K^n . This group may be represented by taking as its elements typical members from each homology class. The identical element of \mathfrak{H}^k is the class of nullhomologous cycles.

In contradistinction to the groups of chains and cycles, none of whose elements are of finite order, the homology group contains, in addition to its identical element, elements of two kinds:—

- (a) cyclic elements A_i^k , corresponding to cycles of which some finite multiple, different from unity, is homologous to zero;
- (b) free elements B_i^k , corresponding to cycles of which no multiple is homologous to zero.

Then the k^{th} Betti number p^k of K^n is the number of such free elements in the base of the group; and the positive integers c_i^k which are such that $c_i^k A_i^k \sim 0$ are the k -torsions of the complex.

The method for determining the Betti and Torsion numbers of K^n is based on the Normal Forms to which the Incidence Matrices of all dimensions of the simplexes of K^n may be reduced. It can be shown that the transformations by which the Incidence Matrices are reduced to their normal form corresponds merely to a new choice of k -chains. The Betti and Torsion Numbers may be read from the normal forms: the Betti number $p^k = a^k - \gamma^k - \gamma^{k-1}$, where a^k is the number of k -simplexes in the simplicial subdivision of K^n , and γ^k is the rank of the matrix H^k ; and the Invariant Factors of H^k are the k -Torsions.

The Euler Characteristic of K^n is defined as being the number $\sum_{r=0}^n (-)^{r+1} p^r$. It may be proved that it is also equal to $\sum_{r=0}^n (-)^{r+1} a^r$.

A fuller treatment of the facts described above is contained in Seifert u. Threlfall, "Topologie," § 15-18, 20, 21, and 23, where proofs may be found. That the Betti and Torsion Numbers, and the Euler Characteristic of K^n are not only independent of the mode of subdivision of K^n , but that they are topological invariants is proved in other chapters of the same volume.

FUNDAMENTAL GROUP.

Just as the homology groups of a complex are bound up with the concept of homology, so the Fundamental Group is bound up with that of homotopy. A "track" in a complex is defined as the continuous image in the complex of a linear segment. Two tracks w_0 and w_1 are "deformable into one another" or "homotopic to one another" if

- (i) to every value of t , $0 \leq t \leq 1$, there correspond in the complex a continuous image $g_t(\bar{w}) = w_t$ of the linear segment $\bar{w} = \overrightarrow{AB}$, such that $g_0(\bar{w}) = w_0$, $g_1(\bar{w}) = w_1$;
- (ii) the position of $g_t(R)$ in the complex, where R is any point of \bar{w} , depends continuously on R , and on t ;
- (iii) $g_t(A) = P$, $g_t(B) = Q$, where P and Q are in the complex, for all values of t .

When one of these tracks, say w_0 , consists of a single point, then w_1 is said to be deformable into zero, or nullhomotopic.

Closed tracks of a connected complex may be assembled into homotopy classes, and these classes form the Fundamental Group of the complex. The nullhomotopous tracks comprise the identical element of the group, which is, in general, not abelian. It can be proved that the Fundamental Group does not depend on the point fixed as the initial point of all tracks, and that it is a topological invariant.

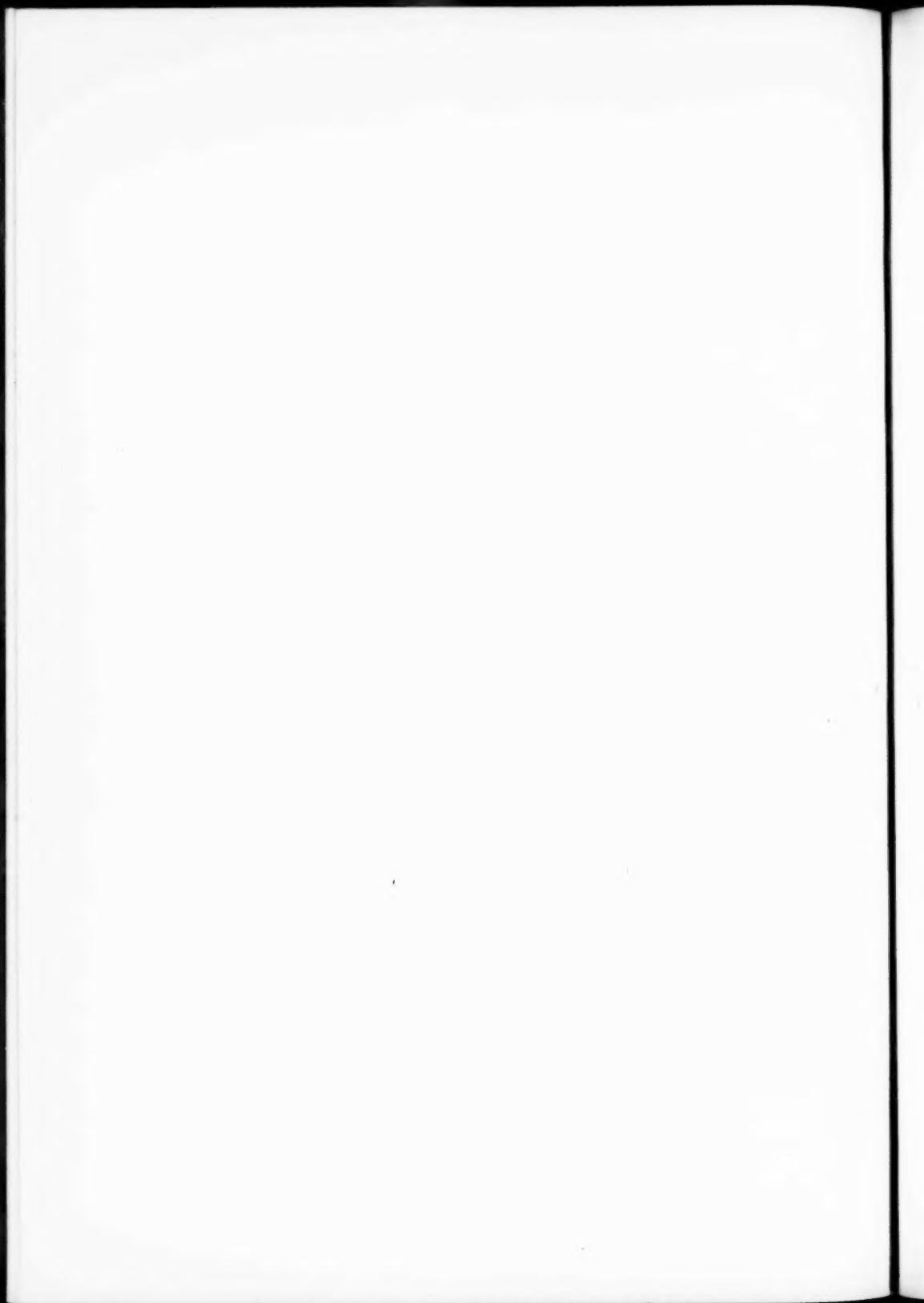
The Fundamental Group may be described by enumerating its generating elements, and stating the relations connecting them. These can be readily obtained for any complex, since the Fundamental Group depends only on the simplexes of dimension 0, 1 and 2. It is not in general isomorphic with the 1-homology group, which is abelian; since homotopy of two chains implies homology, but not *vice versa*.

A full treatment of the Fundamental Group is contained in Seifert u. Threlfall, "Topologie," chapter 7.

POINCARÉ SPACES.

The 3-sphere in euclidian 4-space is defined by the relation $x_1^2 + x_2^2 + x_3^2 + x_4^2 = 1$. It may also be obtained by regarding as identical opposite points with respect to the equatorial plane in the boundary of the set of points defined by $x_1^2 + x_2^2 + x_3^2 \leq 1$. It has no Torsion Numbers, and its Betti Numbers are: $p^0 = p^3 = 1$, $p^1 = p^2 = 0$.

Poincaré Spaces are 3-dimensional manifolds whose homology properties are those of the 3-sphere, but which are not homoeomorphs of the 3-sphere. The existence of Poincaré spaces is a demonstration that homology properties, which are sufficient to distinguish topologically different 2-manifolds from one another, do not suffice for 3-manifolds. The Fundamental Group is therefore a necessary means of distinguishing Poincaré spaces.



SILLIMANITE-CORUNDUM ROCK: A METAMORPHOSED
BAUXITE IN NAMAQUALAND.

By C. B. COETZEE.

(Communicated by A. W. ROGERS.)

(With Plate LI and one Text-figure.)

(Read November 15, 1939.)

The following account deals with the paragenesis of an unusual rock. The analytical tables compiled by Washington (15), Clarke (2), and Hall (9) contain no approximate chemical parallel and the available literature indicates no previous record of a similar rock.

The Occurrence.—The rock outcrops on the Pella R.C. Mission Station in Namaqualand, S. Africa: it is situated 6·2 miles S. 30° W. of the church, and 1·5 miles N. 36° W. of the homestead of Annakoppe. This black weathering exposure forms a conspicuous inselberg (see Plate LI) in the S.W. part of the extensive wind-blown sand dune, which, for a distance up to 5 miles, flanks either side of the sand-drowned Pella river. It is fringed by boulders spawled by insolation from the massive centre, and the whole presents a homogeneous aspect except for certain zones in which either sillimanite or ilmenite predominates. Since the exposure projects from a sand dune the relations to the "basement" rock (which is presumably granite-gneiss) are nowhere visible; and consequently the cubic measurements also are stated with respect to the surface only: length 500 feet, breadth 150 feet, height 35 feet.

On account of its mineralogical composition and texture the rock is extremely tough, and not only resists the collection of material in the field, but also the cutting of sections.

Petrography and Mineralogy.—The macroscopic structure is massive. Sillimanite occurs in fine radiating light brown tufts (of fibrolitic habit) which merge into clear areas and in long colourless cross-fractured prisms, the largest of which measured 2·37 mm. by 26 mm. Colourless corundum forms cores of diameter 5 mm. consisting of aggregated xenoblasts with an average diameter of 0·23 mm. and a maximum of 0·55 mm. Hexagonal outlines, the 0001 parting and polysynthetic twins are occasionally observed. The corundum encloses numerous opaque anhedral of ilmenite ranging from 0·015 mm. to 0·40 mm. over their longer diameters, but in numbers



FIG. 1.—Camera Lucida drawing of sillimanite-corundum rock. Cores of corundum with inclusions of ilmenite (black). The colourless patches are clear sillimanite, and the ruled areas fibrous sillimanite.

the smaller crystals greatly predominate (fig. 1). The optical constants are:—

Sillimanite.	Corundum.
$N_p = 1.654$	Uniaxial negative $N_o = 1.766$ $N_e = 1.761$
$N_m = 1.659$	
$N_g = 1.673$	
$N_p - N_g = 0.019$	∓ 0.002
$2V_z = 30^\circ \mp 1^\circ$ (U.M. Stage)	$N_o - N_e = 0.005$
$= 28^\circ \mp 3^\circ$ (Mallard)	

Chemical Analysis.

SiO ₂	26.01
TiO ₂	5.55
Al ₂ O ₃	66.30
Fe ₂ O ₃	0.41
FeO	0.54
MnO	0.01
MgO	..
CaO	..
Na ₂ O	0.09
K ₂ O	
H ₂ O +	1.00
H ₂ O -	0.08
Total	99.99

Mode.		
Mineral.	By grav. analysis.	By chem. analysis.
Sillimanite .	75.1	70.9
Corundum .	22.0	22.5
Ilmenite .	2.9	6.6
G = 3.34		

Analyst, C. B. Coetzee.

Petrology.—In considering the probable origin of this remarkable rock the latter may be referred to:

1. The recrystallisation of a dominantly aluminous sediment without the addition of igneous material.
2. The interaction between an included fragment and the granite magma. These views are discussed in turn below.

1. *The theory of recrystallisation from a dominantly aluminous sediment* has much to recommend itself. The high proportion of sillimanite and the presence of corundum which has been observed as a contact mineral (1, 3, 8) indicates a metamorphic rock of sedimentary parentage. The composition of the sillimanite-corundum rock (*cf.* Analysis 1) when compared with the average compositions (16) of the main types of igneous, sedimentary, and metamorphic rocks shows a conspicuously lower percentage of SiO₂ and a very pronounced excess of Al₂O₃.

	I.	Analyses recalculated to anhydr. material.			
		II.	III.	IV.	V.
SiO ₂	26.01	26.29	31.06	23.6	21.68
TiO ₂	5.55	5.61	3.02	4.6	5.82
Al ₂ O ₃	66.30	67.02	65.30	68.8	70.84
Fe ₂ O ₃	0.41	0.41	0.42	2.5	1.47
FeO	0.54	0.55
MnO	0.01	0.01
MgO
CaO
Na ₂ O
K ₂ O	0.09	0.09
H ₂ O +	1.00
H ₂ O -	0.08
Totals	99.99	99.98	99.80	99.5	99.61

I. Sillimanite-Corundum rock, Pella. Anal. C. B. Coetzee.

II. Sillimanite-Corundum rock, Pella.

III. Diaspore rock, Jammu, produced by local lateritisation of a clay bed at the base of the Eocene. Anal. J. and H. S. Pattinson (14).

IV. Microferric bauxite, Cazoul (4).

V. Microferric bauxite, La Galline (Alpilles, 4).

The parent rock must consequently have been subjected to secondary conditions which increased the proportion of Al₂O₃ but decreased that of SiO₂, and which produced the nearly complete elimination of Na₂O and K₂O. Such conditions conform to the fundamental theories which account for the genesis of the two principal types of bauxite, viz.:—

(a) The Terra-rossa, Mediterranean, or French type (4), where the bauxite represents a very small insoluble fraction of what was originally a great mass of limestone or dolomite, and

(b) The laterite or Indian type (5), produced by the prolonged subaerial weathering of basaltic lavas, during which process the alkalis and alkaline earths are leached out, while water is being added.

The contention that the Pella rock represents a metamorphosed bauxite is supported by the agreement observed between the composition of the Pella material and the recalculated analyses of the bauxites quoted above. It yet remains to consider whether the bauxite was derived from limestone (dolomite) or from a basaltic type.

The chemical composition supplies no clue in this direction, since

bauxites of different origin may yield entirely similar analyses (2). This similarity becomes accentuated when the analyses are recalculated to anhydrous material, since the smaller percentage of combined water which is broadly speaking diagnostic (5) of the terra-rosa type now becomes deleted. Data in regard to the thickness of the deposits, also, effect no discrimination. Arkansas bauxites (lateritised nepheline-syenite (13)) vary from 10 to 60 feet in thickness (12); those of Parisot, Les Alpilles (which are in genetic association with limestone), have a maximum thickness of 18 metres, an average of 5 to 6 metres, and a minimum of 2 metres (4). The exposed thickness of the Pella occurrence is approximately 35 feet.

Furthermore, TiO_2 enters with equal frequency into the composition of either bauxitic type. In conclusion, the basic granulites and eclogites of this area indicate derivation from calcareous sediments, whereas the amphibole schists like the sillimanite-corundum rock display a high content of titanium.

2. *If interaction between the included fragment and the granite magma is postulated, the fundamental difficulty arises of accounting for the small proportion of alkalis, and for the absence of alkaline earths. Interaction would be concomitant with the introduction of magmatic material (7).*

A corundum-sillimanite rock (in the Norite of the Bushveld Igneous Complex) believed to have originated by interaction between an aluminous sediment and magmatic material is described by Hall and Nel (10). "Through consolidation of the magma these interactions were prevented from completing their normal course, so that a certain transient state became fixed."

Age and Nature of the Metamorphism.—According to present knowledge, the granite and gneiss of the Namaqualand massif which induced the metamorphism of the bauxite were probably intruded at some date between the formation of the Kaaibed (6) of the Swaziland System and that of the Nieuwerust Series of the Nama System. The association sillimanite-ilmenite (11) and the absence of parallelism among the mineral components are suggestive of recrystallisation under conditions of high temperature and great depth.

Relict Textures.—As already stated, the corundum forms aggregates which enclose numerous grains of ilmenite. In regard to the pisolitic structure of bauxites, Fox concludes that the pisolites are composed of amorphous material and generally consist of concentric layers of ferric hydroxide on an aluminous core (5); the alumina, apart from existing as two colloidal hydroxides, also exists in combination with SiO_2 and TiO_2 . From these considerations the corundum-ilmenite cores may be explained as relicts of pisolitic grains or relicts of vermicular aggregates which were composed of aluminous centres holding titanium in combination. An

examination of the plates (4) shows that the diameters of pisolites in French bauxites vary from 0.1 to 55 mm. The corundum cores of the Pella rock have an average diameter of 5 mm., but whatever the size of the postulated pisolites in the bauxite might have been before its metamorphism, it is evident that during their recrystallisation they must have suffered a reduction in volume due to the expulsion of water from the colloidal hydroxides of aluminium.

SUMMARY.

On the Pella R.C. Mission Station in Namaqualand occurs an outcrop of sillimanite-corundum rock. No chemical or mineralogical parallel could be found in the available geological literature.

The analysis yielded: $\text{SiO}_2 = 26.01$, $\text{TiO}_2 = 5.55$, $\text{Al}_2\text{O}_3 = 66.30$, $\text{Fe}_2\text{O}_3 = 0.41$, $\text{FeO} = 0.54$, $\text{MnO} = 0.01$, $\text{MgO} = 0.00$, $\text{CaO} = 0.00$, Na_2O , $\text{K}_2\text{O} = 0.09$, $\text{H}_2\text{O} + = 1.00$, $\text{H}_2\text{O} - = 0.08$. Total = 99.99. The mode is Sillimanite = 70.9, Corundum = 22.5, Ilmenite = 6.6.

The rock is believed to have originated by the static metamorphism of a dominantly aluminous sediment, probably a bauxite.

ACKNOWLEDGMENTS.

The author desires to express his indebtedness to Prof. F. Walker under whose direction the work was accomplished, and to Prof. W. Pugh who placed the facilities of a chemical laboratory at his disposal.

EXPLANATION OF PLATE.

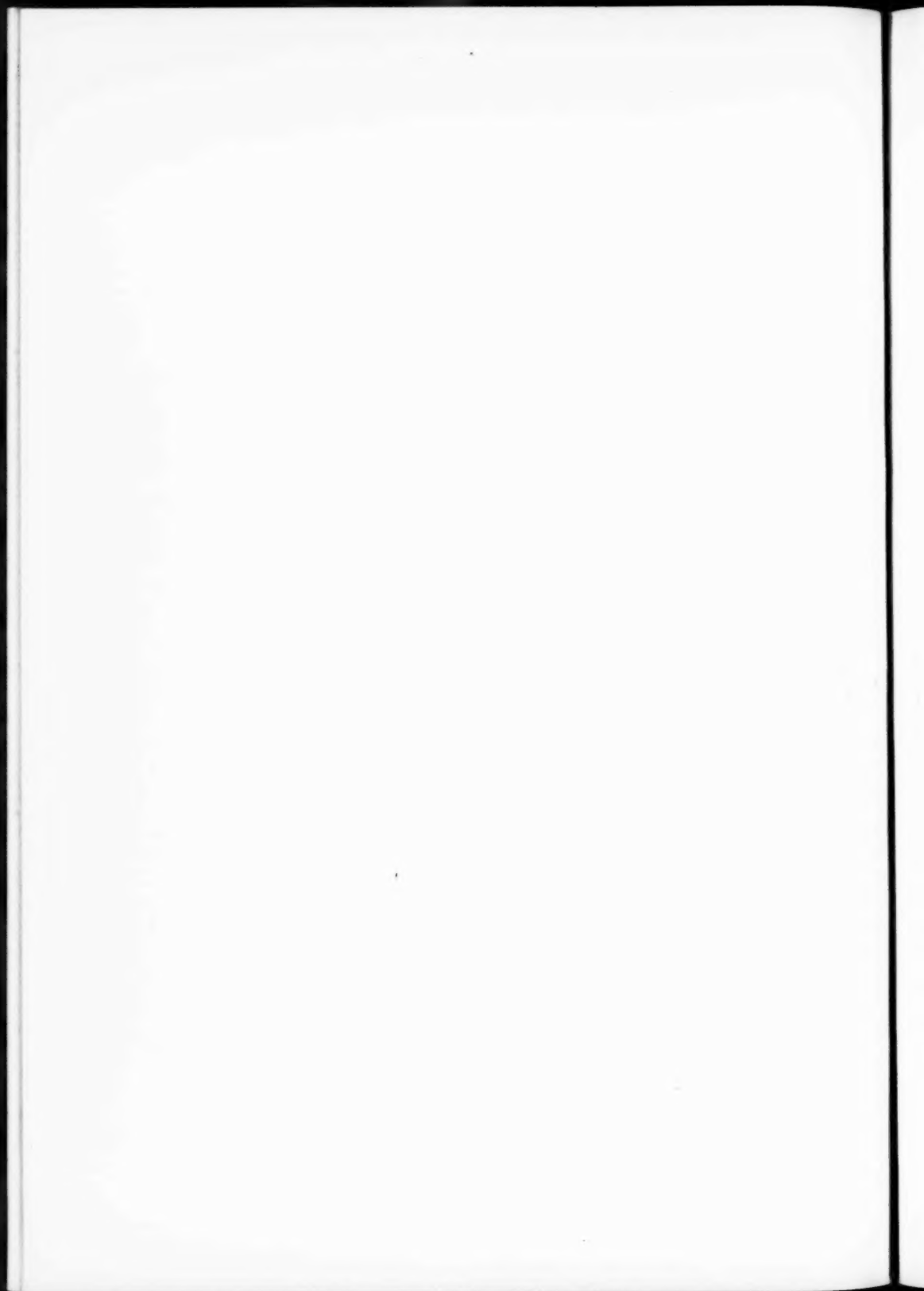
PLATE LI.

Photograph of sillimanite-corundum rock on South Pella.

REFERENCES.

- (1) BUSZ, K., "On the Occurrence of Corundum produced by Contact Metamorphism on Dartmoor," *Geol. Mag.*, p. 492, 1896.
- (2) CLARKE, F. W., "The Data of Geochemistry," U.S. Geol. Surv. Bull. 770, 1924.
- (3) COOMARA-SWAMY, A. K., "Note on the Occurrence of Corundum as a Contact Mineral at Port Paul, near Morlaix (Finistère)," *Q.J.G.S.*, 57, p. 185, 1901.
- (4) DE LAPPARENT, J., "Les bauxites de la France méridionale," *Mém. Minist. Travaux Publics*, p. 81. Paris, 1930.
- (5) FOX, CYRIL S., *Bauxite*. London, 1927.
- (6) GEVEES, T. W., "The Pegmatite Area South of the Orange River in Namaqualand." *Mem. Geol. Surv. S. Afr.*, No. 31, p. 26, 1937.
- (7) GROUT, F. F., *Petrography and Petrology*, pp. 216-220. New York, 1932.
- (8) HALL, A. L., "The Contact Metamorphism in the Pretoria Series of the Lydenburg and Zoutpansberg Districts," *Transv. Geol. Soc.*, pp. 1-24, 1908.
- (9) HALL, A. L., "Analyses of Rocks, Minerals, Ores, Coal, Soils and Water," *Mem. Geol. Surv. S. Afr.*, No. 52, 1938.

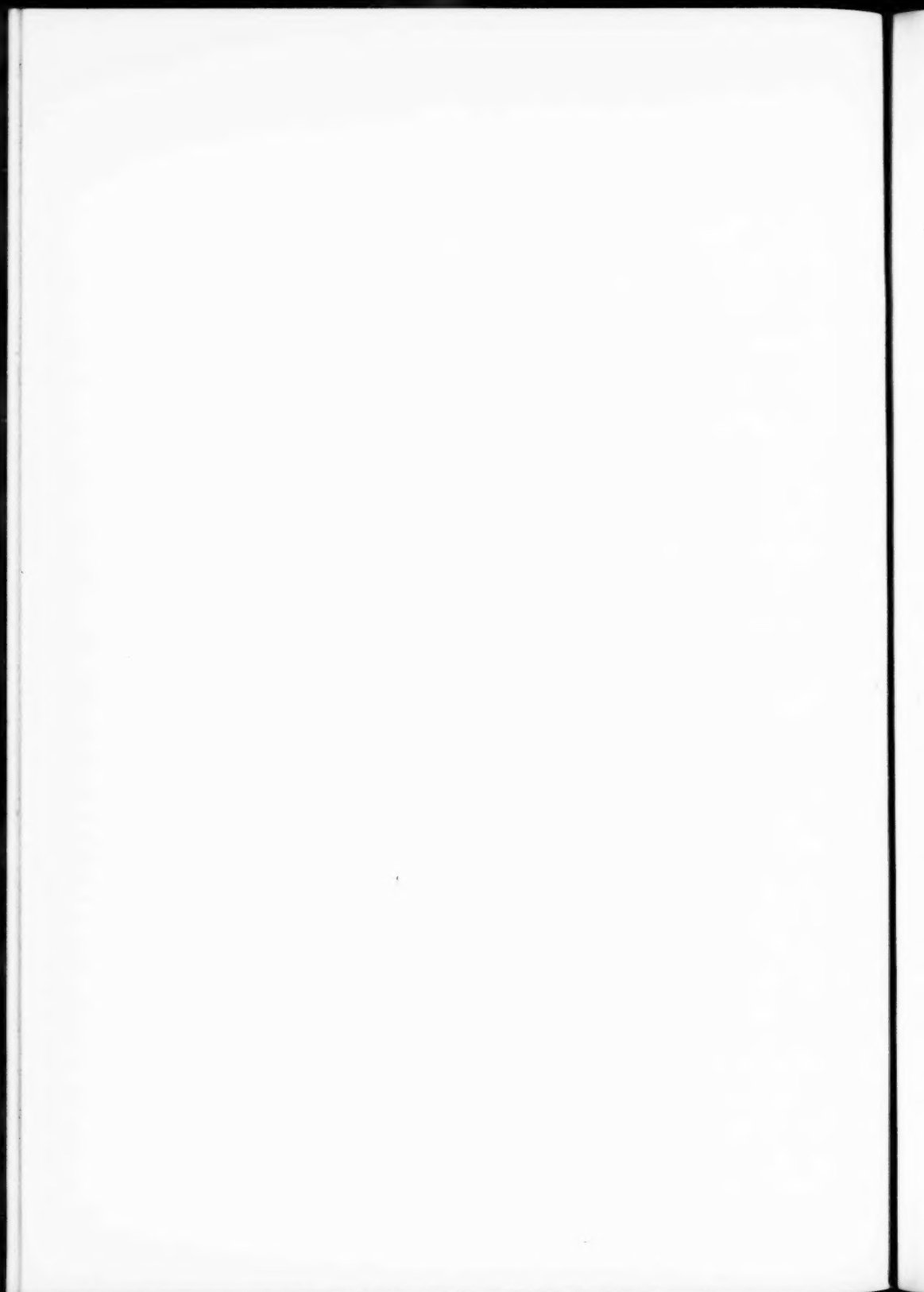
- (10) HALL, A. L., and NEL, L. T., "On the Occurrence of Corundum-Sillimanite Rock in the Norite of the Bushveld Igneous Complex," *Trans. Geol. Soc., S.A.*, 29, 1926.
- (11) HARKER, A., *Metamorphism*, p. 147, 1932.
- (12) LINDGREN, W., *Mineral Deposits*, p. 376. New York, 1933.
- (13) RUMBOLD, W. G., "Bauxite and Aluminium," *Monogr. Imp. Inst.*, p. 93, 1925.
- (14) WADIA, D. N., *Geology of India*. London, 1912.
- (15) WASHINGTON, H. S., "Chemical Analyses of Igneous Rocks," *U.S. Geol. Surv. Professional Paper* 99, 1927.
- (16) *Mem. Geol. Surv. India*, 49, p. 35, 1923.





C. B. Carter.

Scull & Co., Ltd.



THE OCCURRENCE OF BARITE IN AN IRON ORE
DEPOSIT IN NAMAQUALAND.

By MORNA MATHIAS.

(Communicated by A. W. ROGERS.)

(With three Text-figures.)

(Read November 15, 1939.)

INTRODUCTION.

The deposit is situated on the farm "Zuurwater" in the north-eastern portion of Namaqualand (approximate latitude $29^{\circ} 15'$ South and longitude $18^{\circ} 50'$ East).

"Zuurwater" is about 75 miles north-east of Springbok, 24 miles south of the Orange River, and 25 miles from Pella Mission Station. The direction from Pofadder is 79° West of South and from Pella Mission Station 58° West of South. The main road from Springbok to Pofadder passes through the farm "Aggenys," which adjoins "Zuurwater" on the east.

The association of barite with magnetite is rare. This deposit is of particular interest in that the barite appears to be confined to the ore horizon. Along some 1400 yards it constitutes the principal gangue mineral. I have been unable to find any reference in South African publications to a similar type of rock, and believe it to be unique in this country. A search through the available overseas literature has also failed to reveal a comparable deposit.

GENERAL GEOLOGY.

Ancient sediments which probably belong to the Kheis system are represented by recrystallised quartzites, schists, amphibolites and sheared conglomerate. They have all been highly metamorphosed by an intrusive aplo-granite.

The quartzite which contains the magnetite deposit forms a hard resistant capping to the "Inselberge" which characterise the area and rise from the sand-covered flats of the Bushmanland peneplane. The quartzites dip at angles between 22° and 40° , the general direction of dip being north-north-east. The northernmost quartzite mountains extend

as a flat-topped range from east of Aggenys to some 5350 yards beyond the boundary with Zuurwater. They are a conspicuous landmark visible from nearly 20 miles to the south, and form a watershed between rivers flowing north to the Orange River and the inland drainage to the south. The table-top is due, evidently, to a period of peneplanation prior to that of the Bushmanland plateau. The micaceous schists and amphibolites are interbedded with the quartzites. The schists, owing to the greater ease with which they weather, are generally to be found in the valleys and on the lower slopes of the hills.

With regard to the solid geology of the area nothing is known. The author suggests, however, that the successive quartzite ranges, which have approximately the same direction and angle of dip, may be accounted for by the faulting or folding of an originally continuous deposit.

FIELD CHARACTERS OF THE MAGNETITE DEPOSIT.

The iron ore extends in an easterly direction for approximately 3 miles from Swartkop. It occurs in the quartzite along a range of hills, Z2 to Z5, fig. 1, and also in the basal quartzites of the main range.

(a) *Swartkop and the Hills to the East.*

With the exception of Swartkop, which is roughly circular in plan, the hills are elongated, east to west, in conformity with the strike of the sediments. The ore is interbedded with the quartzites and occurs at approximately the same horizon from Swartkop to Z5. The width of the ore bed varies from 4 feet to 10 feet.

Swartkop, so named on account of its black appearance, is an outstanding landmark, and it seems, at first sight, to be composed entirely of iron ore. In point of fact, the iron ore is of limited extent, and the surface features are due to fallen boulders and fragments which litter the hillside. The main concentration of ore is in a bed 8 feet thick intercalated with the quartzites and dipping at 35° in a north-easterly direction. It is composed of massive magnetite and hæmatite with only a slight admixture of quartz. An old working and a well are situated about 30 yards west of the main ore body. A pegmatite cuts the quartzite at this point; it carries spessartite, biotite, muscovite, chalcopryite, pyrite, azurite, and malachite, besides magnetite and hæmatite.

The other portion of the deposit cuts across the bedding of the quartzites, from the top of Swartkop east-south-east to the base. It occurs as an impregnation of the quartzite and carries a far greater percentage of silica than the bedded ore. The dry river-bed north-east of Swartkop and the sandy flats for some distance from the base are littered with boulders of

magnetite. The rock here shows a very fine polished surface due to sand-blasting.

On the northern side of the hill Z2 (fig. 1) the magnetite bed reappears, and here, as well as along Z5, it carries white and pale pink barite as the

Sketch Map of the Farm Aggenys and Part of Zuurwater

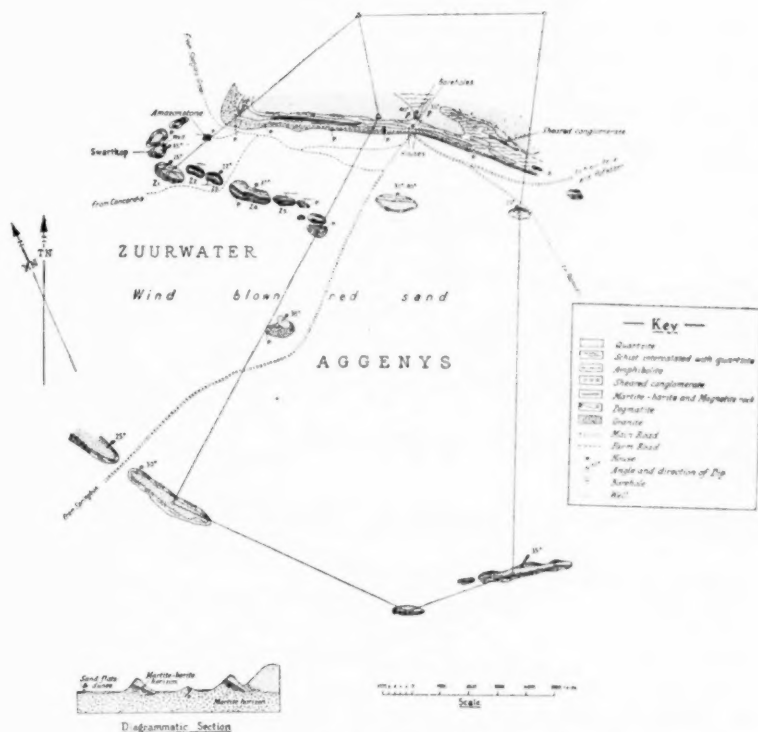


FIG. 1.—Map.

chief gangue mineral. The width of the bed is approximately 6 feet, and the magnetite attains a striking crystal development. Perfect octahedra of magnetite and pseudomorphs in martite, varying in size from 2.4 centimetres to a few millimetres, project from a surface of coarsely granular barite and remnant quartz.

At Z4 the magnetite horizon occurs on the southern slopes of the hill. There is no visible barite here, and the ore has again become massive. The magnetite bed continues along the top of the hill Z5, the ore gradually becoming more disseminated: at the eastern end of the hill it forms veinlets branching through a bed of quartzite 6 feet thick. No further outcrop of magnetite was found east of Z5.

(b) *Iron Ore of the Main Range.*

The main range of quartzites on the farm "Zuurwater" is divided by interbedded schists into two main portions, (a) the high flat-topped mountains, and (b) a belt of hills intersected by river-beds immediately to the south. Magnetite and haematite occur in the latter and extend in the form of a bedded deposit for approximately two miles. The ore is massive and has suffered extensive surface weathering to haematite. The thickness varies between 6 feet and 12 feet. No macroscopic barite was found.

PETROGRAPHY.

All refractive indices were determined on crystals of known orientation by the immersion method, using sodium light and the Leitz-Jelly refractometer.

(a) *Swartkop.*

The iron ore here appears massive in hand specimen and consists principally of magnetite which is often coated with the red oxide, haematite.

Magnetite.—The thin section shows crystals and crystalline aggregates of magnetite which have in part been replaced by pseudomorphs of haematite, i.e. martite. These are set in a ground-mass of quartz. The proportion of iron ore to quartz varies in the main bed from approximately 75 per cent. to 50 per cent. The quartzite above and below also carries a gradually diminishing quantity of magnetite. Many of the smaller magnetite crystals are elongated along the vertical axis. This is due, evidently, to the conditions of growth, as the elongation invariably occurs along cracks in the quartz or boundaries between quartz grains (fig. 2). Some crystals have been entirely replaced to form martite, and are then distinguishable by their reddish-brown colour in reflected light. Martite has frequently formed around the edges of crystal aggregates of magnetite. The size of the magnetite crystals varies from 1.15 mm. to 0.053 mm.; the average size is 0.23 mm.

Quartz forms a mosaic of interlocking grains, most of which show strain phenomena. The average size of the quartz grains is approximately 0.33 mm. The grains vary greatly in size and shape. The largest grain in the section measured 1.24 mm., and the smallest 0.01 mm. An unusual

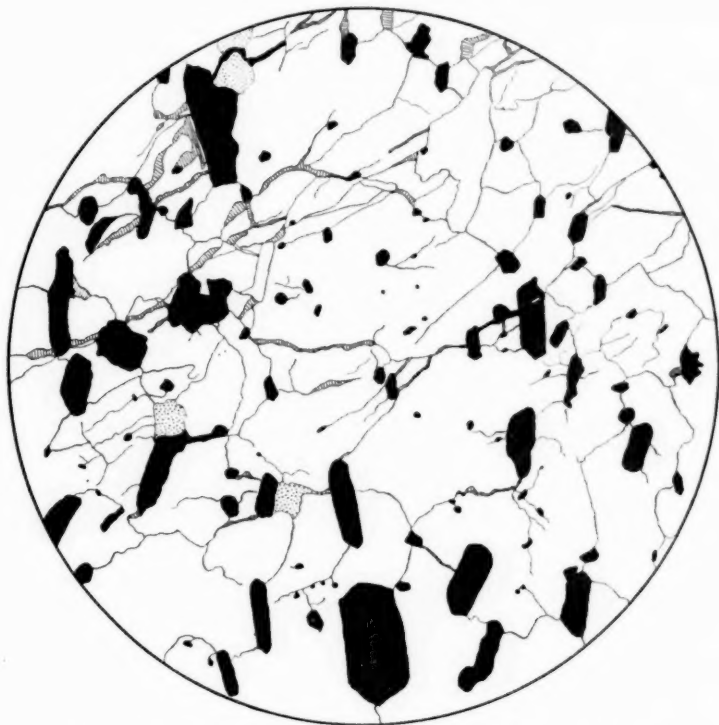


FIG. 2.—Drawing of a thin section of the magnetite-barite rock from Z2, showing the elongation of the magnetite crystals along planes of weakness between quartz grains. Barite is moulded on to two of the magnetite crystals.

Transmitted light \times (40).

Magnetite	= black.
Quartz	= white.
Barite	= dotted.
Iron-stained quartz	= lined.

feature is the abnormal amount of dust-like inclusions, which are probably iron ore. Occasional small prisms of apatite are also enclosed by the quartz: these show good relief, and a few give uniaxial negative figures in convergent light.

Barite is a minor constituent: it occurs as small colourless allotriomorphic grains which are moulded on the magnetite. They measure between 0.14 mm. and 0.03 mm. An analysis was made of the iron content, and the samples were taken from the base, the centre, and the top of the ore bed.

	Base.	Centre.	Top.
FeO . . .	0.17	10.24	9.32
Fe ₂ O ₃ . .	76.11	50.66	48.88

The metallic iron content calculated from these figures is as follows:—

Base . . .	53.36
Centre . . .	43.39
Top . . .	41.43

(b) *Magnetite-barite Bed of Z2 and Z3.*

The texture is coarsely crystalline. Crystals of magnetite and martite, from 2.4 cm. to 0.008 mm. in size, protrude from the weathered surface which is mainly composed of soft barite. The magnetite presents the same features as in the Swartkop sections.

Barite forms allotriomorphic grains moulded on the iron ore (fig. 2): it is interstitial towards quartz (fig. 3). The maximum length observed was 5 mm. and the minimum 0.08 mm. The barite is crowded with minute inclusions, most of which are probably iron ore. It shows typical patchy lustre and good prismatic cleavage. The extinction is straight, and the refractive indices are:

$$\begin{aligned} Z &= 1.647, \\ Y &= 1.638, & Z - X &= 0.010. \\ X &= 1.637, \end{aligned}$$

$$2V_Z \text{ (measured on the universal stage) } = 40^\circ.$$

Quartz.—Nearly all the quartz grains show undulatory extinction; the exceptions being relatively clear recrystallised individuals. The average dimensions of the grains are 0.33 mm. \times 0.49 mm. The quartz along cracks and boundaries between grains is frequently stained by iron oxides, forming what appear to be veinlets of orange and yellow colour.

A sample of the magnetite-barite rock was sent to Mr. F. Herdsman for analysis. The results are tabulated below:

Analysis.

SiO ₂	41.34
FeO	87
Fe ₂ O ₃	37.98
TiO ₂	15
BaO	11.86
SO ₃	6.18
MnO	Nil, or traces
P ₂ O ₅	" "
ZrO	" "
CuO	Nil
	<hr/> 98.38 <hr/>



FIG. 3.—A section from the same rock illustrating the interstitial nature of the barite. Transmitted light $\times (67)$.

Magnetite = black.
 Quartz = white.
 Barite = dotted.
 Iron-stained quartz = lined.

I estimated the water content from a sample taken from the same locality, and found it to be 0.95 per cent. This brings the total to 99.33 per cent.

The composition of the rock corresponding to this analysis is:

Quartz	41.34
Barite	18.06
Ilmenite285
Magnetite	2.49
Haematite	30.60
Limonite	6.58
	<u>99.35</u>

(c) *Eastern End of the Deposit on Z5.*

The hand specimen shows quartzite veined by magnetite. The section reveals clear evidence of dynamic metamorphism. The quartzite has been subjected to great shearing stress, which has caused the quartz to become elongated in a direction at right angles to the stress. A certain amount of granulation has taken place, and the average size of the grains is small, approximately 0.16 mm. in length and 0.04 mm. in breadth. Between crossed Nicols nearly all the quartz shows undulose extinction, and the section appears to have a schistose texture. The magnetite is not nearly so well crystallised as in other parts of the deposit and here forms irregular veinlets replacing the quartz along the planes of schistosity. Martite occurs in minor amount. Barite was not found either in the section or in the heavy residue.

Garnet.—The manganese garnet, spessartite, occurs plentifully in the quartzite. It is mostly colourless in thin section, but some of the larger grains have a faint yellowish-brown tinge. The largest garnet measured 0.18 mm. \times 0.11 mm., and the smallest 0.016 mm. \times 0.015 mm. The average size = 0.04 mm. \times 0.03 mm. The refractive index was determined by immersion in a piperine and iodide melt: $RI = 1.80 (\pm .01)$. In the sodium carbonate bead the powder gave a strong manganese reaction.

Zircon and biotite occur as minor constituents in the quartzite.

(d) *Main Range Ore.*

The ore here is similar to that described at Swartkop, except that no barite was found.

(e) *Associated Quartzite.*

In hand specimen the quartzite is fairly fine grained, and is bluish-grey in colour. It varies little in character either laterally or in its upper and lower contacts with the ore body. The magnetite content decreases gradually away from the contact.

Quartz occurs as a mosaic of interlocking grains from 1.5 mm. to 0.01 mm. in size. It is strained and partially recrystallised. It invariably shows an abnormal amount of duct-like inclusions of iron ore. Apatite is also enclosed by the quartz, and, more rarely, zircon.

Spessartite is abundant. Individual grains are larger than those at Z5, and range in size from 0.03 mm. \times 0.04 mm. to 0.75 mm. \times 0.58 mm. The optical properties of spessartite have already been described.

Mica occurs as prismatic sections and cleavage flakes varying in size from 1.32 mm. to 0.06 mm. The average size is 0.41 mm. It is either brown or green in colour and strongly pleochroic, with the maximum

The Occurrence of Barite in an Iron Ore Deposit in Namaqualand. 215

absorption parallel to Z. Basal plates are isotropic and give a uniaxial negative figure in convergent light.

$$\text{Refractive indices} \begin{cases} \epsilon = 1.600, \\ \omega = 1.571, \end{cases} \quad \epsilon - \omega = 0.029.$$

The green variety of mica is probably an alteration phase intermediate between the brown mica and chlorite. It has similar properties to the brown mica, which is evidently biotite. Much of the mica has been either partially or completely altered to green chlorite. The refractive indices of the chlorite are:

$$\begin{aligned} Z &= 1.598, \\ Y &= 1.587, \\ X &= 1.586. \end{aligned}$$

The bi-refringence is low, $Z - X = 0.013$.

Epidote occurs sporadically as small irregular grains associated with haematite. It is probably partially derived from the biotite. The epidote is bright yellowish-green in colour and has high relief. The grains range in size from 0.16 mm. to 0.01 mm. The average size is approximately 0.05 mm.

$$\text{Refractive indices} \begin{cases} Z = 1.769, \\ Y = 1.753, \\ X = 1.730, \end{cases} \quad Z - X = 0.039.$$

Chalcopyrite occurs plentifully in the quartzite and associated with the iron ore at Swartkop. It was not seen in sections from other parts of the deposit.

Origin.—In considering the question of the origin of the magnetite-barite rock, the following features should be taken into account:—

- (a) The fact that barite is confined to the ore horizon.
- (b) The occurrence of copper ores in association with the iron at Swartkop.
- (c) The nature of the contact with the quartzites, which shows a gradual diminution of iron content.
- (d) The fact that the magnetite transgresses the bedding of the quartzites at Swartkop.
- (e) The veining of the quartzite by magnetite at the eastern end of the outcrop.

These features have led me to postulate an epigenetic origin for both the magnetite and barite. I believe the iron ore to be a metasomatic

replacement deposit introduced into the quartzites from an igneous source at a time when the quartzites were deeply buried beneath younger sediments. The source of the iron was presumably the granite batholith of southern Namaqualand. An aplitic facies of this is intrusive into the schists and quartzites of the area under consideration. Barite is usually formed at a lower temperature than magnetite, and according to the microscopic evidence the barite was introduced subsequent to the magnetite. Barite probably thus represents a later phase of hydrothermal emanation from the same source.

Alternative Theory.—The hypothesis might be advanced that the bedded nature of the deposit suggests a sedimentary origin, and that the barite alone is epigenetic. If this were so, one would expect to find the deposit thinning out towards the end of the outcrop. Actually, it does not do this, but breaks up into bifurcating veins and stringers which seam the quartzite bed. The transgressive nature of the magnetite at Swartkop and the occurrence of copper ores in association with the iron, likewise point to an igneous origin for the magnetite.

A microscopic examination of thin sections from the ore bed proves that the magnetite is of later formation than the quartz. In the case of a metamorphosed ferruginous sandstone, magnetite, being high in the crystalloblastic series, would speedily have assumed crystal form and the quartz would be found filling the interstices between magnetite crystals. Instead of this, one finds that the development of magnetite has been guided by planes of weakness between the quartz grains and cracks in the quartz itself (fig. 2). The possibility of barite being residual seems very remote. Barium sulphate is relatively very insoluble in ground-waters. W. A. Tarr * quotes Clarke as giving 0.05 per cent. barium content in sandstones and shales. It is difficult to see why descending solutions, even supposing they could concentrate sufficient BaSO_4 , should deposit their content within a quartzite bed, and not have penetrated to a point where they came into contact with some less pervious formation.

ECONOMIC ASPECTS.

A rough estimate of the available tonnage of iron ore shows that approximately 46,000 tons are exposed at the surface. This does not allow for the persistence of the ore bed in depth. The grade of the ores is slightly less than that of the iron ore from the Lake Superior region which contain approximately 50 per cent. to 60 per cent. of iron. At Zuurwater the deposit averages 42 per cent. metallic iron. This is well within the minimum tenor for iron ore quoted by W. Lindgren † (i.e. 30 per cent.).

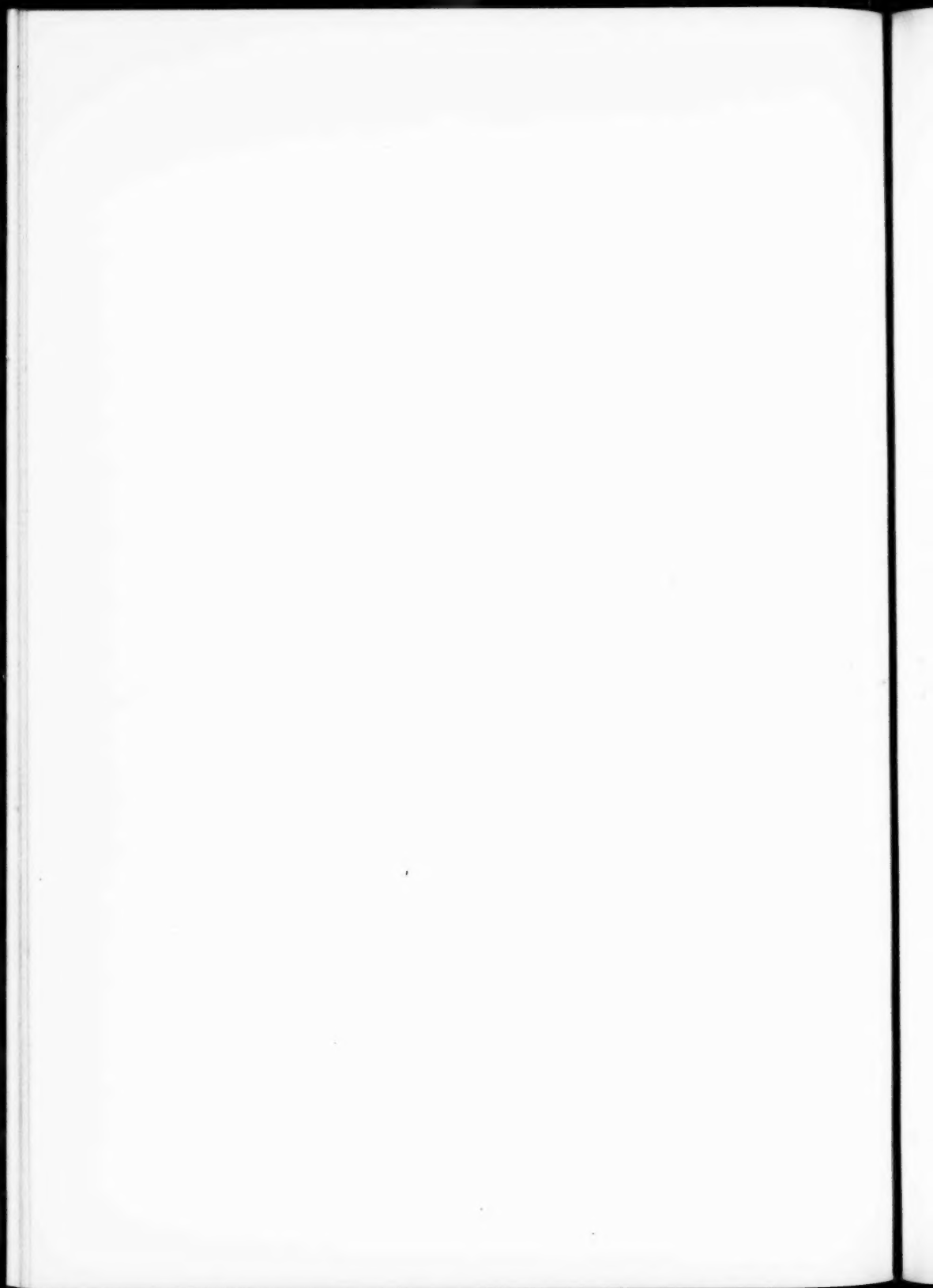
* W. A. Tarr, "Barite Deposits of Missouri," *Econ. Geol.*, vol. xiv, 1919.

† W. Lindgren, *Mineral Deposits*. New York, 1928.

but the deposit cannot be considered an economic proposition on account of its inaccessibility and small reserves. It is situated 62 miles from the nearest railway station at O'okiep and 118 miles from Port Nolloth which is the nearest seaport.

ACKNOWLEDGMENTS.

I am very grateful to Dr. F. Walker, Professor of Mineralogy and Geology at the University of Cape Town, for his guidance and invaluable assistance in every branch of my work. I am also greatly indebted to Major J. G. W. Leipoldt for directing my attention to the magnetite deposit, and for his advice and unfailing kindness to me in the field. In addition, I should like to thank Dr. W. Pugh, Head of the Department of Chemistry at the University of Cape Town, for according me facilities for chemical analysis.



THE RECENT ARCHAEOLOGY OF GOKOMERE, SOUTHERN RHODESIA.

- I. A DESCRIPTION OF THE SITES AT GOKOMERE, SOUTHERN RHODESIA.
By T. GARDNER, S.J.
- II. A STUDY OF THE POTTERY FROM GOKOMERE, SOUTHERN RHODESIA.
By L. H. WELLS, M.Sc., M.B., Ch.B., and J. F. SCHOFIELD, A.R.I.B.A.
- III. A STUDY OF THE BEADS FROM THE TUNNEL SITE, GOKOMERE, SOUTHERN RHODESIA. By J. F. SCHOFIELD, A.R.I.B.A.

(With ten Text-figures.)

(Read September 20, 1939.)

I. A DESCRIPTION OF THE SITES AT GOKOMERE, SOUTHERN RHODESIA.

A Description of the Site.

The kopje at Gokomere is about 10 miles to the north of the town of Fort Victoria in Southern Rhodesia. The massif is encircled by a series of large boulders, corner stones, and cornices, dislodged from above in the course of the years. Many of these boulders provide shelter from the cold winds and the rain, and "*de facto*" not a few of them were used as houses by the men of the Stone Age. The four chief shelters face the four cardinal points, and these have been closely examined during the last fifteen years. The excavations have provided data which may perhaps prove to be useful to those who are working out the problem of our Middle Stone Age group of industries. In addition to this, two of the shelters have yielded the pottery which is the subject of this study.

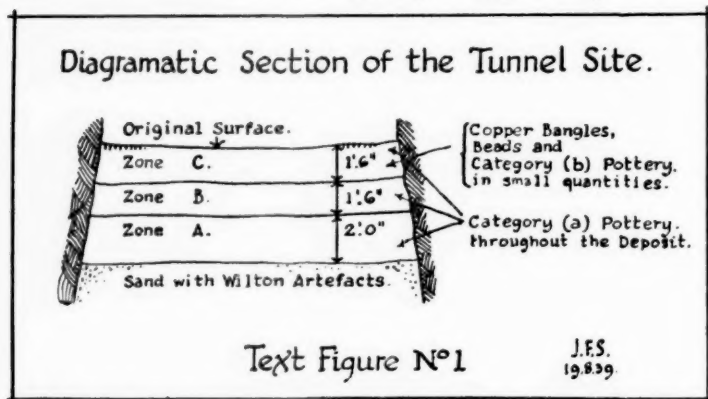
The Tunnel Site.

This site is at the west end of the kopje, at its base. It is formed by elongated boulders that lean against one another. The floor follows the slant of the hill. The tunnel is about 20 yards in length. The mouth and a wide area extending outwards were found to be occupied by a group of submerged boulders, of which the largest apparently rest on the bed rock, some 20 feet down.

We opened our main trench outside the entrance, parallel to the base

of the hill and 40 feet to the front. This trench was 70 feet in length, 6 feet in width, and it carried us down to a depth of 17 feet. Then, in order to get to the mouth of the tunnel, we excavated an intervening area 40 feet in length by 20 feet in width. Finally, we took out a section across the mouth of the tunnel, pyramidal in form, with the apex at the bottom.

Since this preface deals only with the pottery, it will be sufficient to state that the upper layers consisted of midden debris, which was 2 feet deep at the main trench and 5 feet deep at the entrance of the tunnel. There, specimens of pottery occurred in plenty. The sand beneath the midden carried Wilton artefacts sparsely, through a depth of some



20 inches. We had constantly to remove big blocks of granite as we worked down through the midden, and their removal disturbed the soil around them, interfering with the registration of the depth of the pieces of pottery which were found. However, for the other pottery, we can certify that the specimens submitted to the experts in ceramics have their true depth assigned to them, being taken from one of three zones, viz.:—

Zone A, 2 feet in thickness, directly above the Wilton layer.

Zone B, $1\frac{1}{2}$ feet in thickness, directly above Zone A.

Zone C, $1\frac{1}{2}$ feet in thickness, directly above Zone B.

The lowest sherd in Zone A was found precisely at the junction of the midden and the sand carrying the Wilton artefacts (2, 1). The decorated sherds in this zone were comparatively few.

The beads and the bangles of flat, spirally wound copper wire were found only in the upper part of Zone C.

A section of the deposits in the Tunnel Site is shown in fig. 1.

The Cave Site.

The Cave Site has a frontage of from 30 to 40 yards at the eastern end of the kopje. In plan it resembles a dumb-bell, the southern end of which is a small cave, and the northern is a shelter which is protected by a granite canopy.

On excavation of the cave, it was discovered that the soil consisted of three distinct strata. The lowest of these was rich in the relics of the Wilton Culture. Directly above this, and completely sealing it, there was a relatively hard and well-laid floor of bright yellow dagga, which had a thickness of between 2 and 3 inches. Above this floor there was a thin layer of midden material.

In the shelter at the northern end of the site, the sequence of the strata was somewhat similar, with the exception that the bright yellow dagga floor was absent. Its place was taken by a drab-coloured layer which appeared to be a bed of ashes which had been left by the Wilton folk, and which, when wet, had been trampled down to a surface which was even and hard for a depth of about 3 inches. Directly above this there was a layer of midden material which had a thickness of about 4 feet 6 inches.

It was from this layer that the fragments of pottery were collected which Caton-Thompson identified as belonging to the Class "A" pottery from Zimbabwe. In addition to this pottery a large number of small objects were also recovered from it which may be described briefly as follows:—

From the uppermost stratum, 12 inches in depth—

Several pieces of deeply rusted iron work, including an axe, $7\frac{1}{2}$ inches by $1\frac{3}{4}$ inches; an assegai blade, $3\frac{1}{4}$ inches by 1 inch; an arrow head with two barbs, $5\frac{1}{2}$ inches from point to tang; an oval ring, and a small spatula-shaped knife.

A metal bead and two small metal rings, all probably of copper. The bead weighed $\frac{1}{4}$ ounce and showed no sign of having been joined. The larger ring weighed $\frac{1}{8}$ ounce and the place where the ends of the metal had been joined could be seen quite clearly. The smaller ring had been made by bending a piece of wire round, without any attempt to join the ends.

Near the surface of the midden, several fragments of very thin pottery were found—

A "divining bone" in wood, several spikes of bone about 4 inches in length, of which some had been rubbed smooth, and some small pieces of bone which had been perforated for use as pendants.

In the middle stratum, also 12 inches in depth, the little pot was found (7, 2), and at a slightly higher level there was a maize cob which showed signs of having been burnt.

The remainder of the midden contained nothing of interest, being made up of ashes and bone fragments.

To the investigator, the most striking feature of this site was the way in which both of the floors drew a definite line between the Stone Age and the Iron Age. There was no Stone Age work above that line, nor were there any sherds below it.

No correlation between the Tunnel and the Cave Site could be established, except that both rested on a stratum which contained Wilton artefacts.

The Dam Site.

This site is at the head of a dry spruit where, during the excavation for a dam, a stratum of pot-clay, 7 feet in thickness, was encountered; alongside this, and at a depth of 4 feet below the base of the pot-clay stratum, the sherd illustrated (7, 3) was found. From these circumstances, it would appear to be of an undoubted antiquity. Indeed, Dr. Frobenius' party described it as being "Babylonian."

II. A STUDY OF THE POTTERY FROM GOKOMERE, SOUTHERN RHODESIA.

INTRODUCTION.

This report is based on a collection of sherds sent to the Department of Anatomy, University of the Witwatersrand, by the Rev. Father T. Gardner, S.J. The collection comprises portions of about 140 different vessels. Of these 15 were obtained from the deepest portion of the deposit (Zone A), 17 from Zone B, and 33 from the uppermost layer (Zone C). The remainder came from the shallower unstratified portion of the deposit.

Description of the Pottery.

A. *Fabric and Firing.*—The clay contains numerous small particles of quartz, and occasionally larger angular and sub-angular fragments, ranging up to 5 mm. in diameter. No indication of the use of the wheel is visible, and it is evident that the vessels were entirely hand-moulded. No trace of the coil method of construction could be discovered, and it is probable that all but the smallest vessels were built up by the addition of successive pieces or "bats" of clay. The thickness of the walls ranges from 6 mm. to 15 mm., averaging 10 mm. to 12 mm. There is, however, considerable variation in the thickness of the wall of a single pot at different points, nor is the average thickness less in small than in large vessels.

As the degree of firing was sufficient only to effect cohesion of the particles, it is probable that the ware was baked upon an open fire; there is no trace of even partial fusion, or of vitrification. A fresh fracture almost invariably shows a laminated structure, the external layers being baked to a harder consistence than the core of the sherd.

There is considerable variation in the colour of the fired clay. The majority of the sherds have a dark grey core, the surface layers being either a lighter grey or a brown, occasionally with a reddish tinge. In a smaller number of cases the core has a brown or even a definitely red colour, while the surfaces are a light brown, or even grey. As a result of these variations the natural surface colour of the sherds shows a wide range from grey through various shades of brown to a pale red. From the fact that in some cases different fragments from the same pot show a considerable difference in the degree of firing, it is probable that much of this colour variation is due to accidental secondary burning.

B. Forms.—The homogeneous character of this pottery makes any decision of the nomenclature of the types used a matter of uncertainty, for when, for example, every step in the transition from a shouldered pot to a shouldered bowl, or from a deep bowl to a neckless pot is represented, it is exceedingly difficult to determine exactly where one type ends and the other begins. Nevertheless, the majority of the vessels can be classified primarily as pots and bowls, with due provision for sub-division.

(1) *Pots.*—This group is by far the larger, and as this term has such a wide application, we do not propose to use it without further qualification. To this end we propose to use the following sub-divisions of the parent group.

(a) *Shouldered Pots.*—These pots, which form the mass of our material, may be described as being pots in which the lip was turned upwards to form a more or less pronounced neck. The bodies were in some cases approximately spherical; but more frequently they were sub-spherical, that is to say, the height was less than the diameter, which ranged from 8 to 16 inches.

From the fragmentary condition of much of our material, it is often difficult to decide on the original shape of the body, and thus we are often in doubt as to whether a particular piece should be grouped with the pots or the bowls; indeed, in many cases, our only guide was the fact that the interior surface, which in a bowl was commonly burnished, was of necessity left plain in a pot.

The neck usually rose from the body with a gradual curve, but occasionally there was a sharper transition. The upper part of the neck was vertical, or even flaring—in a few cases exaggeratedly so. The height was usually medium, less commonly short, and occasionally relatively tall. The diameter of the aperture ranged from 6 to 12 inches. The mouth was in every case wide in proportion to the diameter and height of the pot.

The treatment of the rim in these pots shows considerable variety. In some cases it was rounded and tapered, in others it was cut off square. Still more commonly, there was an external moulded rim-band from $\frac{1}{2}$ to 1 inch in depth, with a flat or slightly convex surface. This rim-band

ended in some specimens by passing into the general surface of the neck, but in others it was sharply cut off. The rims were always more or less tapered above, being usually rounded, but sometimes squared. In a few specimens which are apparently confined to the latest portion of the deposit (5, 3 and 6) the rim-band assumed the form of a prominent cylindrical roll.

(b) *Neckless Pots*.—Neckless pots are extremely rare, and have been noted only in Zone C (6, 4). They were spherical, a foot or more in diameter, with a wide aperture surrounded by a rim-band which, in the example illustrated, merged into a band of comb-marks. The rim itself was tapered and finished with a ridge.

(c) *Miniature Pots or Pipkins*.—Of this type, three examples are present (2, 5; 2, 8; and 3, 7). The bodies were spherical, about 3 inches in diameter, and the necks were either vertical or everted. The fact that these vessels were carefully finished and decorated suggests that they may have been designed for some formal use, *e.g.* some recent Bantu peoples use such vessels for containing relishes.

(2) *Bowls*.—This group shows such a large variation, both in the diameter of the mouth and in the height of the vessels, that we propose to sub-divide it into the following types:—

(a) *Shallow Bowls*.—The first type, which however is uncommon, is the shallow bowl or dish, in which the maximum depth is not more than one-third of the diameter. These vessels have a diameter of 9 inches or more, with a flat base and up-turned margins, the rim being vertical or everted (8, 7).

(b) *Deep Bowls*.—Much more numerous, constituting the greater part of this group, are the deep bowls, in which the maximum depth is not less than half the diameter. Some resemble the shallow bowls in having the sides vertical throughout, while in others, which may be termed basin-shaped bowls, the sides are everted (8, 10). In a greater number, however, the diameter of the mouth is less than the maximum diameter of the vessel, so that the bowl has a distinct shoulder and thus may aptly be described as being shouldered bowls. One specimen (5, 7), shows an exaggeration of this form and might be described as a belled bowl.

Amongst the deep bowls there is a sub-group which is further distinguished by a carinated or sub-carinated form. The upper part of the bowl (above the carination) usually has a concave profile. This portion may be everted or contracted, or it may assume the appearance of a cavetto moulding between the carination and a markedly everted lip (7, 1). The carinations vary from being well-marked features (7, 4 and 8), to being hardly perceptible. In every case it is confined to the better type of bowls. The sub-carination is found on the coarser bowls where it was probably a structural rather than a decorative feature.

Another sub-group is represented by two examples (6, 10 and 12) with tall and almost vertical sides. These belong to the type which Schofield has termed "Beaker" bowls, the profile of the sides being identical with that of the beaker type of vessel, but the diameter, in relation to the height, being much greater.

The treatment of the rims of these bowls follows much the same lines as amongst the pots, except that the rim-band is usually decorated. In one example (5, 9), the rim-band was combined with the neck to form a band of unusual width. In two examples, the rim itself was decorated with a few lines of comb-marks (5, 10; and 7, 6). We also find that the flattened rim combined with a projecting rim-band is much in evidence (8), and that amongst the carinated and sub-carinated bowls the rim had commonly a curious internal projection, which we have not met with elsewhere; although one example amongst the pots (4, 9) points in a similar direction.

To conclude this description of the forms, it is to be noted that the collection contains no examples of bases, feet, handles, lugs, or rim-holes, while the only suggestion of a spout is in the notching of the rim of a small bowl (7, 1).

C. Finish and Decoration: (1) *Finish*.—The majority of the vessels of the most usual types were smoothed with the hand alone, a smaller number have a matt finish, and a still fewer number are definitely burnished. The unusual vessels, on the other hand, are usually burnished, and less frequently have a matt finish. The interior surface of many of the sherds was found to be very rough indeed; it may be suggested that this is due to decay rather than to a careless finish.

The matt and burnished fragments are either grey, black, buff, brindled, or of a warm brown to purple colour. While a number of these pieces show streaks of graphite, there are a few examples (3, 3; and 8, 5) which show more; in these, the whole of the interior surface and the rim-band appear to have been burnished with graphite.

It was also noticed that in a number of cases the interior surface of the bowls and their rim-bands had been burnished, while the remainder of the surface had either been smoothed or given a matt finish.

In the whole collection there is no example of a polychrome treatment.

(2) *Method of Decoration*.—All but a very few of the vessels in the collection were more or less elaborately decorated by moulding, impressions, incisions, or not unusually by a combination of some or all of these media.

(a) *Moulded Ornament*.—This, apart from the varieties of rim treatment, is rare, the commonest form being the raised ribs, which encircled the necks of some of the vessels, more particularly those of the carinated bowls.

(b) *Impressed Decoration*.—This is the principal method employed in this ware. In the majority of cases, it takes the form of a series of

rectangular impressions, probably executed with a comb. From the size of these impressions, it is to be inferred that the comb was commonly made of wood, or of some similar material. From the upper layers, however, examples are not lacking of a much finer type of impression, which was probably produced with a metal implement.

In a number of cases, individual impressions, which appear to have been made with a circular or an angular stylus, were used in decoration. One or two sherds show irregular impressions which suggest that an uneven string of beads had been used (2, 10). In one instance, a twisted strand of wire appears to have been used (2, 5). There are no examples of cord or finger-nail ornamentation.

(c) *Incised Ornament.*—This usually takes the form of broad furrows, probably made by dragging a comb over the surface (4, 3, 4, 5 and 6), or by scratching the pot with a blunt stick (4, 1 and 2); more rarely it is made with a blade or a point (2, 9). All incisions were made on the wet clay.

(3) *Disposition of Decoration.*—With rare exceptions, decoration on these vessels is confined to the rim, neck, and shoulder, or to corresponding parts of the pots. The following varieties in the disposition of the decoration have been noted:—

- (a) The rim-band alone decorated (2, 2 and 3).
- (b) As last, but with a line of comb-marks or incisions along the shoulder (2, 6; and 5, 8).
- (c) The rim-band plain, with a broad band of ornament encircling the whole depth of the neck (4 and 6).
- (d) The rim-band decorated, and a band of ornament encircling the neck (3).

The neck ornament is frequently divided into a series of bands by strongly marked horizontal impressions. When these last are very deep, the bands may appear in profile as flat ribs (3, 2 and 3). The occasional horizontal moulded bands are an exaggeration of these ribs (3, 6). In a few instances, the lowest band is treated with a different motif from the remainder (7, 8), or is left plain (4, 7).

Two sherds in the collection show ornament applied to the upper surface of the rim (5, 10; and 7, 6). Ornamentation of the shoulder is limited to the bowl with the festoons (7, 1).

(4) *Patterns of Decoration.*—The patterns produced by these various motifs and their combinations with the dispositions of the decorations are naturally extremely varied. The illustrations include examples of all the patterns observed, and call for no detailed description here. Certain generalisations are, however, possible:—

- (a) Generally the ornament is rectilinear; but several examples of curvilinear motifs are present (2, 7; 4, 2; 5, 3; 5, 6; and 7, 1).

- (b) Decoration applied to the rim-bands invariably takes the form of oblique lines, usually of comb-marks, but occasionally incised (2, 9).
- (c) Though herring-bone pattern is common, alternate hatching is very unusual (5, 7).
- (d) Outline triangles occur on only two sherds (3, 8), and hatched triangles are not represented at all.

DISCUSSION.

We believe that the pottery from the Tunnel Site at Gokomere can be classified as belonging to the following categories:—

- (a) The main bulk of the pottery from all Zones, including that decorated with large comb-marks (probably made with a wooden comb). The principal types being shouldered pots, neckless pots, bowls, basins, etc.
- (b) The pots from Zone C, decorated with fine comb-marks, probably made with a metal comb (2, 7; 3, 8; 5, 3; 5, 6; and 8, 1, 2 and 3); this ware may have been developed from the foregoing at Gokomere, or it may be an imported ware; but there can be no doubt but that it belongs to the same fundamental class.

General Design.—It is evident from Father Gardner's account of the Tunnel Site, that the pottery he collected was ordinary household refuse, and that because of this, the coarser types of utensils should predominate in it. We found, in fact, that well-finished pieces are few and far between, for the bulk of the material is made up of common domestic wares.

Now, it is probable that these well-finished pieces were made for particular purposes, and perhaps for particular persons in the community. It is also probable that because of this, they represent traditional designs, both in shape and decoration, and that these would only be partially expressed in the pottery in common everyday use. This is illustrated very clearly in the three features which we shall proceed to discuss.

(1) *The Rim-band.*—The rim-band is a feature which, in one form or another, is found on nearly every one of our pots. We believe, however, that the tendency was for the rim-band to disappear, and whilst on most of the vessels it has a well-marked projection, on others it is merely vestigial or is merged in the neck (2, 4, 7, 8 and 10; and 4, 1). It was further noted that, with few exceptions, all the shouldered pots have decorated rim-bands, while all the bowls have plain rim-bands, and that while the former usually had a convex profile, amongst the latter it had, very commonly, a flat projection. It is also evident from several examples (8, 5 and 8) that these flattened rim-bands had been made by tapering the clay of the rim while it was wet, folding it down on the outside and then trimming off the surplus clay, thus giving a sharply defined line to the

junction of the rim-band with the neck. This technique tended to produce that squarishness of rim profile which is seen in many of the bowls, but it never entirely replaced the simpler rounded form which was frequently finished to a well-defined ridge on its upper aspect (8, 4 and 6).

At Gokomere only two examples of decorative rims were found (5, 10; and 7, 6). At Mapungubwe three bowls were taken with decoration worked on the rims after the ware had been burnt. At Touppe, in Bechuanaland, several rims were found which had been decorated with the comb in the same way as the rims from Gokomere, but the profile of these rims is akin to the internally bevelled rims from Mapungubwe. This internal bevelling, which is a striking feature of the bowl rims at Mapungubwe, Parma, and Touppe, is represented amongst our wares by only one rather poor example (7, 5).

(2) *Neck Decoration.*—It will be seen from our description of the bowls and the shouldered pots, that the necks are sometimes decorated and sometimes plain, and that since both types occurred in the same stratum, it is clear that both were being made and used at the same time. It is suggested, however, that although this is the case, the pots with the decorated necks represent an earlier stage in the pottery tradition than the others, for the reasons which are stated below.

It will be found that the decoration of the necks of all the better-finished bowls and pots was done with well-defined bands or projecting ribs, which were picked out with oblique lines or comb impressions. Since the formation of these ribs was a matter of some difficulty, and only the better-class vessels were treated in this way, it is highly probable that such were reserved for the use of persons of importance, and for this reason would be made in accordance with primitive traditions and practice. It is natural to suppose that when common pots were required, these, if decorated at all, would be treated in a simplified manner. This is exactly what we find, for in the common practice, the more elaborate ribs were replaced by lines of comb-marks, drawn across a background which was filled in with lines arranged in the various ways shown in our illustrations (4, 1).

This treatment of the neck appears to have developed into a type from which all trace of the horizontal divisions had disappeared, and the neck was covered with multiple comb-marks (5, 4 and 5), vertical comb-lines (4, 4; and 7, 9), or diagonal lines (4, 8). In another variation, the neck was encircled by a chevron in deep comb impressions on a background of large comb-marks arranged vertically (3, 4). This, it is suggested, may have given rise to the form in which the only neck decoration was a series of large chevrons in double lines, occupying the whole space between the rim-band and the shoulder.

(3) *Carination and Sub-carination*.—The carinated form is, in this collection, restricted to the finely made bowls, and may well be a decorative motif which had its origin in a structural process, such as a technique in which the body and the neck were made separately and then joined together. In all the examples before us (7, 4, 7, 8, 9; and 8, 2) the ridge has, just above it, either a line or band of comb-marks, or a line of stylus impressions. At Echo (1) and on the Limpopo sites we found that the carination was similarly decorated. On the latter sites the carinated form was unusual, but it was noted that even when it had not been used, the line of comb-marks had been retained (Pl. XXVII, 2). It is interesting to find the same tendency in a number of our pots, for they, too, frequently have a line of comb-marks along the shoulder, in a precisely similar manner to the pots from Bambandyanalo and Parma. Sub-carination, on the other hand, is not restricted to the finer pots (8, 4), but is of fairly common occurrence.

From the foregoing we conclude that in their ancestral form our pots and bowls had a carinated profile, with comb-marks along the ridge, a well-marked rim-band, and a neck decorated with several slightly projecting horizontal ribs, each of which was picked out with oblique lines or comb-marks.

Other Pottery Types: (1) *The Basin-Bowls*.—These vessels indicate very clearly the tendency, which we have already noted, to make the mouth of a disproportionate width in relation to the height. This resulted in the walls of the deep bowls being inclined outwards until a basin-shaped vessel was achieved (8, 9, 10, 11). This tendency was not as marked at Gokomere as it was at Echo, for on the latter site a piece was taken in which the process had been carried to its logical limit, and the rim was horizontal. As might be expected from the conservatism of the potters, the decorated rim-band was retained in its traditional position, but could be seen only when the basin was turned mouth downwards.

(2) *The Bellied Pot*.—This piece (5, 7) has a deep black burnish and decorative detail, which makes it so similar to pottery from Mapungubwe (Pl. XXI, 2) that it is clear it has been influenced by the pottery tradition termed Class M₁ at that site; and which Schofield has included in his classification under the symbol R₂. But in spite of these similarities, the profile of the rim-band and the possession of the decorated neck-band are entirely consistent with our Category (a). We consider, therefore, that we have in this piece an example of the blending of these two pottery traditions.

(3) *The Festooned Bowl*.—This bowl (7, 1) is very different from the rest of the wares from this site, both in its profile and in its decoration. It is, therefore, possible that it belongs to a distinct though related pottery tradition.

(4) *The Neckless Pots*.—These pots deserve our attention because they illustrate the tendency towards the spherical pot, which we have found to be universal in South African Native ceramics of a Bantu facies. It is therefore interesting to find that this type was confined to the uppermost Zone of the deposit, and that all the examples which survived belonged to Category (a) of our wares.

(5) The Sherds illustrated, 6, 7, 8; and 8, 11, may also belong to a different ware, but until we have more comparative material at our disposal, we prefer to consider them as unusual variants on the common theme.

The Pot from the Cave Site.—The little shouldered pot (7, 2) is so different from any of the wares from the Tunnel Site, that it must be described separately. It was finished with a black burnish. At three equidistant points around its shoulder two shallow depressions divided by a central vertical ridge were made. On the upper margin of these depressions, a line of three small pellets was placed in a position which was in line with the band of diagonal hatching which ran round the shoulder of the pot. It seems that these depressions were produced by pressing the tips of two fingers into the wet clay, and pushing them up towards the shoulder of the pot. The pellets were then placed in position. If this was the case, then from the size of the impressions, it is to be inferred that the potter was of small physique, and so probably a woman.

This pot unquestionably belongs to the pottery which has been classified as R_{3a} (p. 331, 1), and finds its nearest counterpart in the "Dimpled Ware" from Echo.

The Fragment from the Dam Site.—This sherd (7, 3) appears to be a fragment from a shouldered pot which had been decorated along the shoulder with a line of shallow triangular impressions. It does not resemble any other pottery in this collection, but it is not distinctive enough to attempt to classify it in the present state of our knowledge. The decoration, however, shows a certain resemblance to the sherd illustrated by Caton-Thompson, Pl. LXIX, 12 (3). We do not think that there is any evidence which would tend to support the Babylonian origin which has been suggested for our sherd.

Comparative Material : Zimbabwe.—In seeking among the pottery types of South Africa for material comparable with that from Gokomere, it is natural, in view of the proximity of the site to Great Zimbabwe, to commence with the pottery of that place as described and classified by Caton-Thompson (p. 25, 3). This author has herself identified pottery from the Cave Site, Gokomere, with her Class A, which she describes as follows:—

"A coarse red-brown to dark grey hand-made ware, gritty with quartz particles and badly fired; the rims have a flat overturned lip . . . , and they are sometimes decorated with diagonal or other arrangements of

shallow square or round impressions in the wet clay. In other cases the lip is plain and the decoration appears as a band on the neck."

A comparison of this description with that of the Gokomere pottery just given, and of Caton-Thompson's figures, Pls. XVIII, 1, and LXIX (3), with those accompanying this paper leave little doubt of the correctness of this identification.

The remains of Class A pottery from Zimbabwe were all in small fragments, and no attempt was made to reconstruct the forms of the original vessels. The Gokomere material furnishes us for the first time with definite information regarding the forms of these vessels. These included shouldered pots, some of very large size, neckless pots, pipkins, a variety of bowls, and some other occasional forms, including carinated vessels.

It may be noted that among unpublished sherds from Zimbabwe in the South African Museum, Cape Town, obtained by Bent in his excavations, there are a number of Class A fragments larger than any published by Caton-Thompson. These represent pot forms closely similar to those from Gokomere.

Echo Farm.—On the Echo Farm site near Salisbury, Southern Rhodesia (fig. 1 (1)), several pieces were found that have a close resemblance to some of our wares. The shouldered pot (2, 10) has its counterpart in the Echo material and the same applies to the pot with a rim-band decorated with diagonal incisions (2, 9). The bearing of the basin and the carinated pot from this site on our pottery has already been discussed.

Bambata Cave.—During the excavations in 1919 (4) a fragment of the rim of a large shouldered pot was found which resembles 2, 10, but a stamp made of coiled wire appears to have been used in decorating the rim-band and the neck has double parallel scratches at inch centres.

Que-Que.—Three surface finds from Que-Que are in the Rhodesian Museum, the one a fragment of a shouldered pot, similar to 4, 1, and evidently, from its condition, of a considerable age. Another is part of a bowl similar to 8, 12, but with the decoration impressed with beads. The third is a shouldered pot somewhat similar to our Category (b) and probably recent.

Gulubahwe Cave, Matopo Hills.—This was another surface find of a fragment of a shouldered pot decorated with bold horizontal lines.

Dhlo-Dhlo.—Caton-Thompson records having found a sherd of Class A pottery as follows:—

"We cut away the lower cement floor and cleared out the underlying stone filling. The only objects found in it were a few sherds of ware similar to the fabric of the pots above, two black graphic-polished sherds, and a welcome fragment of the decorated rough red ware found at Zimbabwe" (p. 174, 3).

This infilling rested on a fine sand "full of flakes and quartz debris."

Madiliyangra Rock Shelter.—The pieces illustrated by Neville Jones (Pl. VIII, 5) include fragments of two small pots similar to our 10, 2, but with the neck decorated with bold horizontal lines. A fragment of the rim of a neckless pot, similar to 6, 4, but decorated with incised lines. A fragment of the rim of a bowl, similar to 6, 6. Fragments of the neck of a small vessel in a thin ware, decorated with fine comb-marks, very similar to 5, 4.

Arcturus, near Salisbury.—The pottery from this site appears to have been unearthened during the clearing out of some old workings. It includes four shouldered pots with everted rims, and one with an almost vertical rim, all made in a rough style, which, although it belongs to the same class as our wares, is more nearly related to the material from Echo. With these pots there were four bowls which are quite unlike anything from Gokomere.

Neikerk Ruins.—MacIver has illustrated several pieces which clearly belong to our wares, notably on Pl. XI, 4 (6). It would appear from the text that these were excavated at the "Place of Offerings."

Maonza Cave, near Umtali.—A rim fragment, similar to 2, 1, was found in this cave.

Parma Kopje.—A rim fragment, illustrated Plate XXXII, 7 (2), was excavated from beneath a "Cement" floor in a rock shelter at this site.

Limpopo Sites.—The pottery from the Limpopo Sites has by no means the same degree of similarity to our wares which we have remarked elsewhere, but we believe that the pottery classified as M₂ belongs to a related tradition, consideration of which may be left to the forthcoming volume of reports dealing with those sites.

Salisbury Commonage.—A fragment of our ware was found in a rock shelter on Salisbury Commonage, towards the base of a deposit which had a maximum depth of 3 feet 9 inches. With it there were numerous implements of a Wilton facies. These implements were also found throughout the deposit, with the exception of the surface layer, but associated with a kindred type of pottery which has been classified as R_{1a} (7).

A GENERAL DISCUSSION.

The pre-history of Southern Rhodesia during the last phase of the Late Stone Age is still very obscure. Any site, therefore, which can throw light on the period when the ancient inhabitants of the country were coming into touch with the newer ways of the Iron Age must engage our serious attention.

At Gokomere there is no doubt as to the course of events, for, as Father Gardner has put it in writing of the Cave Site:—

"To the investigator, the most striking feature of this site was the way in which both of the floors drew a definite line between the Stone Age and the Iron Age. There was no Stone Age work above that line, nor were there any sherds below it."

The same may be said of the Tunnel Site, where the break between the two Ages is equally definite although it is not emphasised by any sort of a floor. At Madiliyangwa and Bambata, although the sequence of the events was the same, pottery occurred only in the layer of surface dust and debris which was no more than a few inches in thickness. At Salisbury Commonage, on the other hand, the pottery was associated with, or intercalated in, late Stone Age deposits. The events at Nyazongo (8) seem to be similar to those at Salisbury, with the added complication of the presence of ground stone tools amongst the Wilton material.

We must conclude, therefore, that although at Gokomere there was a clear-cut break between the two occupations, the break was of such short duration that there was no time for the accumulation of a noticeable quantity of sterile deposit.

At Salisbury and Nyazongo the conditions cannot be explained so simply and suggest that either the Stone Age occupants of the shelters were in close contact with a pot-making and iron-working people over a considerable period, or else that the change from the Stone to the Iron Age was accompanied not by a change in the inhabitants of the place, but by a change in the ideas of a population which ethnically may have remained unchanged to any large extent. This latter view derives some support from the course which events took at Mapungubwe, where a people who were almost entirely non-Bantu in their physical type were practising a culture which in its principal aspects is fundamentally that of the present-day Bantu.

The history of the Iron Age occupation can be divided into two distinct periods, the earlier of these being represented by the deposits in the Tunnel Site and in the Cave Site.

The pottery from the first of these can be again divided into the Categories (a) and (b). The former should unquestionably be included in Class R₁, for not only do the details of the decoration and the form of the vessels in the collection resemble those of that class, but we have much evidence to show that both were subject to similar tendencies in form and design.

The pottery which we have included in Category (b) (2, 7; 3, 8; 5, 3; and 8, 1, 2, 3) all came from the uppermost stratum of the deposit, and it differs very considerably from the bulk of the collection. The ware on the whole is finer, a buff, grey, or brindled finish predominates, the rim-bands are more definitely convex in profile, and the comb-marks of the

decorations are usually curved and appear to have been made with a thin metal comb.

It is impossible to say at present whether this type of pottery was developed at Gokomere, or whether it was imported from elsewhere. Although it does not conform to the Class R_1 tradition in all respects, we believe it has more affinities to that class than to any other, and have, therefore, included it therein.

As will be seen from a reference to Section III of this paper, this pottery was associated with imported glass beads which can be dated with some certainty as being not earlier than the last decades of the eighteenth century.

The second period is represented only by the little shouldered pot (7, 2) from the Northern Shelter at the Cave Site.

Unfortunately, the deposits in this shelter cannot be directly correlated stratigraphically with the midden in the Southern Cave, for although Caton-Thompson identified fragments of pottery from the shelter in her Class A pottery, exact particulars of the find are lacking; but it is reasonable to suppose that the deposits are later because they partially obstructed the access to the cave; and this surmise is entirely borne out by an examination of the list of the cultural material associated with the pot, and more particularly by the presence of the maize cob. It is true that the earliest recorded occurrence of maize in South Africa occurs in the account of the survivors of the wreck of the *Nossa Senhora de Belem* who, in 1635, found the plant growing in the neighbourhood of Port St. Johns (p. 205, 9). It is unlikely, however, that it spread inland until a much later period, and as all the other materials, including the little pot, show unmistakably similarities to modern native practice, there can be little doubt but that the whole deposit belongs to the nineteenth century, although no datable objects were contained in it.

We are still entirely unable to give any account of the antecedents of our Class R_1 wares before it appeared as a fully developed entity on so many of the archaeological sites over the length and breadth of Southern Rhodesia. As to its subsequent history, Schofield has suggested that it was the ancestral pottery of a branch of the Sotho people.

The beautiful wares of the Class R_2 types are entirely absent at Gokomere, and their influence can only be traced in a single bellied bowl. In view of the proximity of Zimbabwe, where this widely distributed pottery was plentiful, this state of affairs may seem strange, but we must remember that all barbaric cultures tend to be very localised, and the general insecurity and lack of communications favour the retention of parochial traditions long after their general disappearance.

There are also no examples of the polychrome wares of the Roswi-Venda peoples, although they again are in evidence at Zimbabwe. Indeed

Gokomere seems to have been a backwater which was left unruffled by the great events of the eighteenth century, which resulted in the setting up of the Mambo dynasty in Southern Rhodesia.

A SUMMARY OF CONCLUSIONS.

From the foregoing we conclude:—

(a) That the superimposition of a deposit containing a pottery-using culture upon the remains of a late Stone Age industry, without the interposition of a sterile layer, shows that the succession of these cultures was not interrupted for any long period of time.

(b) That the bulk of the pottery recovered from the Tunnel Site coincides with wares from Zimbabwe and from other sites which have been termed Class A pottery. It is proposed to include all this pottery under the symbol of Class R_1 .

(c) That the Class R_1 pottery on this site may have been contemporaneous with wares that have been termed Class R_2 , as an example of fusion between the two classes of pottery was noted. The single sherd from Parma suggests the possibility that it was also a contemporary, in part at least, with the Class M_2 pottery of the Limpopo sites.

(d) That while no date can be assigned for the beginning of the occupation of our site, the termination of that occupation may be dated as being not earlier than *circa* 1830, for the beads of the later class from Zone C belong to that period.

(e) It has been suggested that Class R_1 and Class R_2 pottery belonged respectively to branches of the Sotho and Shona cultural groups. Nothing has been discovered on this site which would tend to invalidate such a conclusion. If this is indeed the case, this deposit would indicate that people practising a Sotho culture were in occupation at Gokomere long after the Shona and the Roswi-Venda had established themselves in the surrounding territory, and that this occupation of our site persisted up to about the time of the Swazi and the Matabele invasions, by which it was probably terminated.

III. A STUDY OF THE BEADS FROM THE TUNNEL SITE, GOKOMERE, SOUTHERN RHODESIA.

DESCRIPTION OF THE BEADS.

Glass beads were found at the Tunnel Site only in the upper part of Zone C. These beads belonged to seven types:—

- (1a) Irregular cylinders of cane glass, opaque Indian-red on a deep green transparent base, 6×9 mm.
- (1b) Irregular cylinders of cane glass, opaque Indian-red on a light green transparent base, 4×5 mm. to 7×9 mm.

- (1c) Irregular cylinders of cane glass, opaque Indian-red on a light blue base, 7×11.5 mm.
- (2) Irregular cylinders of cane glass, transparent crackled colourless glass over an opaque white base, about 7×9 mm.
- (3) Oblates of opaque pink glass, 2×4 mm.
- (4) Irregular oblates of cane glass, transparent crimson over an opaque white base, 5×5.5 mm. to 2×3 mm.
- (5) Hexagonal bead of violet cane translucent glass on a base of light blue glass, 7×10 mm.

DISCUSSION.

The most striking feature of these beads is that they fall into two distinct classes, of which the earlier comprises types (1a), (1b), (1c), and (2), while the latter comprises types (3), (4), and (5).

The Earlier Beads.—The beads which we have included in Type (1) are probably all variants of a common theme. An example of the smaller variety of (1a) was found by Caton-Thompson under circumstances which were suggestive of some antiquity, but, on the other hand, identical beads were imported into Africa by the shipload during the closing decades of the eighteenth century and even later. Type (2), the "crackled white" bead, is probably of a similar date; it is unlikely to be any earlier, because one was found in the rock shelter on the Acropolis (A, 4, No. 48) with other objects, which are properly regarded as amongst the latest objects found at that place (pp. 82 and 233, 3, and 82, 6).

The Later Beads.—The pink beads are definitely late, that is subsequent to 1830. They do not appear in the Northern Transvaal until after the time of Mzilikazi's invasion, and it is probable that they have a similar date in Southern Rhodesia. Type (4) is the *Mungazi* of the Venda canon, and its name, derived from the Zulu *iGazi*, meaning blood, suggests that it was probably introduced by the Matabele. Type (5) is the *Denga* of the Venda, and was certainly being imported up to 1850 and probably later (p. 108, 2, and 354, 10).

GENERAL DISCUSSION AND CONCLUSIONS.

From the foregoing account of the Pottery and the Beads, we believe that it will be apparent that Gokomere is to be considered as being strictly contemporary with Zimbabwe, for the pottery of our Category (a) belongs to the same class as the earliest wares from that place, while our beads reflect its latest phase. It is, therefore, a remarkable fact that although the two sites are only 28 miles apart, the beads of our First and Second Series should be well represented at Zimbabwe and entirely absent at Gokomere.

It is interesting to find that similar conditions obtain on the Limpopo Valley Sites, for the beads of the First and Second Series were found in quantities at Mapungubwe, but the sub-pavement material in Rock Shelter No. 1 at Parma, which is probably a contemporary site, did not yield a single specimen. More than this, we find that such neighbouring sites as Mapungubwe Hill and Bambandyanalo display wide divergences in the types of beads used by their ancient inhabitants.

We believe that it would be difficult to account for this localised use of beads unless we recognise that in the olden days the distribution of beads was very strictly controlled, probably by a taboo system. Some traces of this seem to have survived amongst the Venda and the Pedi, who restrict the use of their old beads to members of their chief's families.

The fact that our Earlier and our Later beads are found together may be due to the survival of the former as heirlooms, a practice of which we have many extant examples, or to the way in which beads, owing to their small size, their smoothness of surface, aided by the domestic efforts of rodents and even insects, tend to be worked down into midden material. We must not exaggerate the effects of this stratigraphical displacement, for not only were Zones A and B at Gokomere entirely free from beads, but even in Zone C they were found only near the surface. Further, since the date of the earliest and of the latest type found differ approximately by only half a century, their presence together lends force to our belief that the site at Gokomere was probably abandoned not earlier than the third decade of last century.

REFERENCES.

- (1) SCHOFIELD, J. F., "Pottery from the Salisbury District, Southern Rhodesia," *Proc. Roy. Soc. S. Afr.*, vol. xxvi, pt. iv, 1938.
- (2) FOUCHÉ, LEÓ, *Mapungubwe, Ancient Bantu Civilization on the Limpopo*. Cambridge, 1937. Part III. Work Done in 1934: Pottery. By J. F. Schofield. Part IV. Report on Beads. By H. C. Beck.
- (3) CATON-THOMPSON, G., *Zimbabwe Culture*. Clarendon Press, Oxford, 1933.
- (4) ARNOLD and NEVILLE JONES, "Notes on the Bushman Cave at Bambata, Matopos," *Proc. Sci. Assoc. S. Rhodesia*, vol. xvii, pt. i, 1919.
- (5) NEVILLE JONES, *Occasional Papers of the Rhodesian Museum*, No. 2. Bulawayo, 1933.
- (6) RANDALL-MACIVER, D., *Mediaeval Rhodesia*. London, 1906.
- (7) SCHOFIELD, J. F., "Salisbury Commonage Sites," *S. Afr. Journ. Sci.*, vol. xxix, pp. 772-777, 1932.
- (8) MARTIN, C., *Occasional Paper*, No. 1. Queen Victoria Memorial Library, Salisbury, 1938.
- (9) THEAL, G. M., *Records of South-Eastern Africa*, vol. viii. London.
- (10) SCHOFIELD, J. F., "A Preliminary Study of the Prehistoric Beads of the Northern Transvaal and Natal," *Proc. Roy. Soc. S. Afr.*, vol. xxvi, pt. iv, 1938.

DESCRIPTION OF TEXT-FIGURE NO. 2.

1. A fragment of the rim of a shouldered pot or bowl, 11 inches over the rim, in a grey clay with a matt surface. The rim was rounded, and directly below it there was a projecting rim-band with a convex section, decorated with bold diagonal comb-marks. This piece of pottery was the lowest taken on the Tunnel Site. From Zone A. Class R_1 .

2. A shouldered pot or bowl, 12 inches over the rim and about 9½ inches in height, in a coarse reddish clay, with a reddish buff to grey matt surface. The rim was rounded and had a slightly thickened rim-band, decorated with diagonal comb-marks with a line of comb-marks directly below it. From the unstratified midden, Tunnel Site. Class R_1 .

3. A shouldered pot, 9 inches over the rim in a grey clay with a grey matt surface. The rim was rounded and had a slightly projecting convex rim-band which was decorated with diagonal comb-marks. From Zone A, Tunnel Site. Class R_1 .

4. A shouldered pot, 9 inches over the rim, in a grey clay with a smooth grey surface. The rim was rounded and slightly everted. From Zone A, Tunnel Site. Class R_1 .

5. A fragment of the rim of a pipkin, 4 inches over the rim, in a grey clay with a grey surface, burnished externally and matt internally. The rim was rounded and had a narrow rim-band which was tilted out and decorated with diagonal impressions, apparently made with a twisted wire. From the unstratified midden, Tunnel Site. Class probably R_1 .

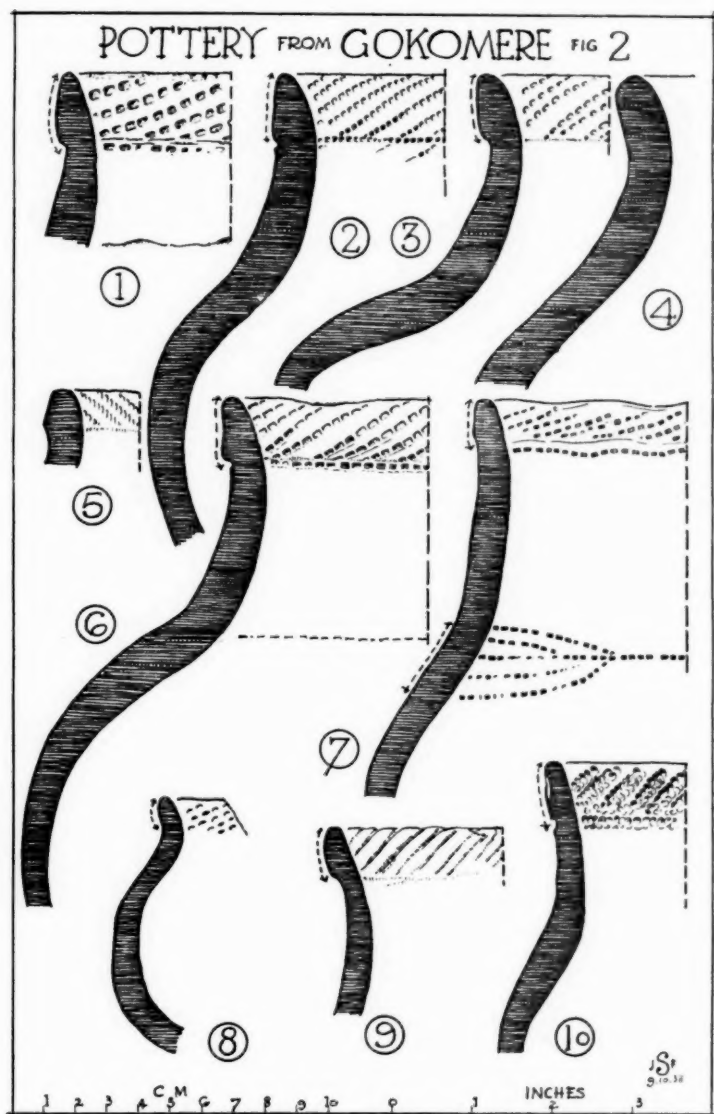
6. A shouldered pot, 7½ inches over the rim, in a grey clay with a grey matt surface. The rim was rounded and had a narrow, slightly projecting and concave rim-band decorated with diagonal comb-marks and a line of comb-marks below it. There was a line of similar impressions on the shoulder. From Zone B, Tunnel Site. Class R_1 .

7. A shouldered pot or bowl, 11 inches over the rim, in a grey clay with a buff matt surface. The rim was rounded, slightly flared and apparently scalloped. The rim-band was decorated with diagonal comb-marks. The shoulder had a line of similar impressions which was expanded over a portion of its length into a lenticular band formed with four lines of comb-marks. From Zone C, Tunnel Site. Class R_1 .

8. A small pipkin in the form of a shouldered pot, 3½ inches in diameter with a height of about 3½ inches, in a reddish clay with a black burnish externally and a grey finish internally. The rim was rounded and slightly flared, and decorated with a band of diagonal comb-marks. From Zone C, Tunnel Site. Class R_1 .

9. Fragment of the rim of a pot or a bowl, 10 inches over the rim, in a grey clay with a black matt surface externally and a grey finish internally. The rim was rounded; the convex rim-band was decorated with diagonal lines which had been cut on the wet clay. From the unstratified midden, Tunnel Site. Class R_1 .

10. Fragment of the rim of a shouldered pot, 6 inches over the rim, in a grey clay, with a matt surface externally and a smooth finish internally. The rim was rounded and the neck was slightly flared. The rim-band was formed with diagonal impressions, probably made with a string of beads, below this there was a line of similar impressions. From the unstratified midden, Tunnel Site. Class R_1 .



DESCRIPTION OF TEXT-FIGURE NO. 3.

1. A shouldered pot, $6\frac{1}{2}$ inches over the rim, in a grey clay, finished externally to a brownish grey matt surface. The interior is very much corroded. The rim was rounded and had a slight external projection. The concave neck was decorated with three bands between four lines of comb-marks. The two upper bands were filled in with diagonal lines, and the lowest band with horizontal lines, all of which were cut on the wet clay. From Zone C, Tunnel Site. Class R₁.

2. A shouldered pot, about 8 inches over the rim, in a gritty grey clay, with a smooth finish. The rim was rounded, flattened and everted. The rim-band was plain, and separated from the concave neck by a deep groove which was probably made with a comb. Similar grooves divided the neck into three unequal bands. The two upper bands were decorated with diagonal comb-marks which were very indistinct, and which ran in alternating directions. From Zone A, Tunnel Site. Class R₁.

3. A shouldered pot or bowl, $9\frac{1}{2}$ inches over the rim, in a grey clay with quartz inclusions. The interior and the rim were burnished with graphite, and the remainder finished to a black matt surface. The rim was rounded and flattened, and had a slightly projecting rim-band, below which the neck was concave and was decorated with three bands of incised diagonal lines on the wet clay. These bands were separated by lines of comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

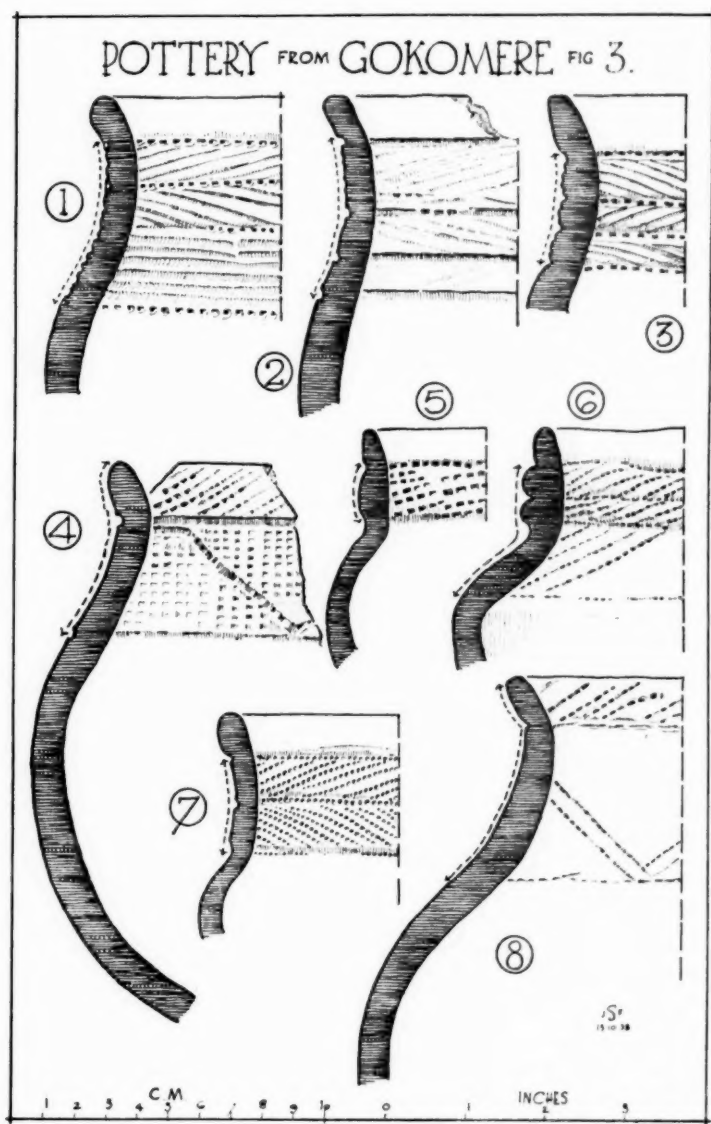
4. A shouldered pot, about $6\frac{1}{2}$ inches over the rim, in a grey to light red clay, finished to a brindled buff surface externally. The interior is much decayed. The rim was rounded and slightly everted, and the neck was concave. The rim-band was decorated with diagonal comb-marks, and was separated from the neck by a deeply incised line. A similar line separated the neck from the shoulder. The neck was covered with rough square comb-marks in vertical lines, and over these a deeply incised chevron had been made with rough comb-marks. From Zone B, Tunnel Site. Class R₁.

5. A pot with a short vertical neck, 5 inches over the rim, in a gritty grey clay. The exterior and the upper part of the neck internally were burnished black, and the remainder was finished to a black matt surface. The rim was rounded and the rim-band was slightly convex. Below it there was a convex band of diagonal comb-marks between two lines of the same. All were made in a very rough manner. From the unstratified midden, Tunnel Site. Class R₁.

6. A pot with a short vertical neck, 7 inches over the rim, in a coarse grey clay, finished to a grey matt surface externally, and smoothed internally. The rim was rounded, and the rim-band was slightly convex. The neck had two boldly projecting convex bands decorated with diagonal comb-marks with lines of the same separating the bands. Below the neck, the shoulder was decorated with groups of four diagonal comb lines, and the shoulder was emphasised with a similar line. All were made in a very rough manner. From Zone B, Tunnel Site. Class R₁.

7. A pipkin, 4 inches over the rim, in a gritty grey clay, finished matt, with the exception of the body, which was burnished black. The rim was rounded, and had a convex rim-band. The neck was decorated with two projecting bands of diagonal comb-marks between three comb lines. From Zone B, Tunnel Site. Class R₁.

8. A shouldered pot or bowl, about $10\frac{1}{2}$ inches over the rim, in a grey clay finished to a brindled matt surface. The rim was rounded, flattened and everted, and had a rim-band decorated with roughly made diagonal comb-marks. A line of similar comb-marks ran round the shoulder. The neck was concave and decorated with chevrons, formed with two lines of comb-marks. From Zone C, Tunnel Site. Class R₁.



DESCRIPTION OF TEXT-FIGURE NO. 4.

1. A shouldered pot or bowl, about 9 inches over the rim, in a grey clay with a smooth grey surface. The rim was rounded, and the rim-band was brought forward to form a slight ridge, and was decorated with diagonal comb-marks. The neck, for a width of 2½ inches, was covered with light horizontal lines, which were made by scraping it with a comb; further, this band had comb lines at its upper and lower edges and in its centre. From Zone A, Tunnel Site. Class R₁.

2. A shouldered pot or bowl, about 11 inches over the rim, in a coarse grey clay, finished to a smooth brown surface. The rim was rounded and flattened, and had a slightly projecting rim-band. The neck had a band, 2 inches in width, of shallow horizontal lines, apparently made with a comb having six teeth. Below this band there was another, decorated with small arches, which had been made, very roughly, with a similar comb. From Zone C, Tunnel Site. Class R₁.

3. A fragment of a shouldered pot, about 5 inches over the rim, in a grey clay with a dark brown surface, matt externally and smoothed internally. The rim was rounded, the rim-band was flush and decorated with diagonal comb-marks. The neck was concave, directly below the rim-band was a line of point marks, the remainder of the neck was covered with horizontal lines, divided into panels with vertical lines, of which only one has survived. From the unstratified midden, Tunnel Site. Class R₁.

4. A fragment of a shouldered pot or bowl, about 11 inches over the rim, in a gritty grey clay with a dark brown matt surface externally and a smooth buff surface internally. The rim was rounded and had a slightly convex rim-band decorated with diagonal comb-marks, below this there was a line of comb-marks, which had been continued on to the neck by drawing the comb vertically downwards. From Zone C, Tunnel Site. Class R₁.

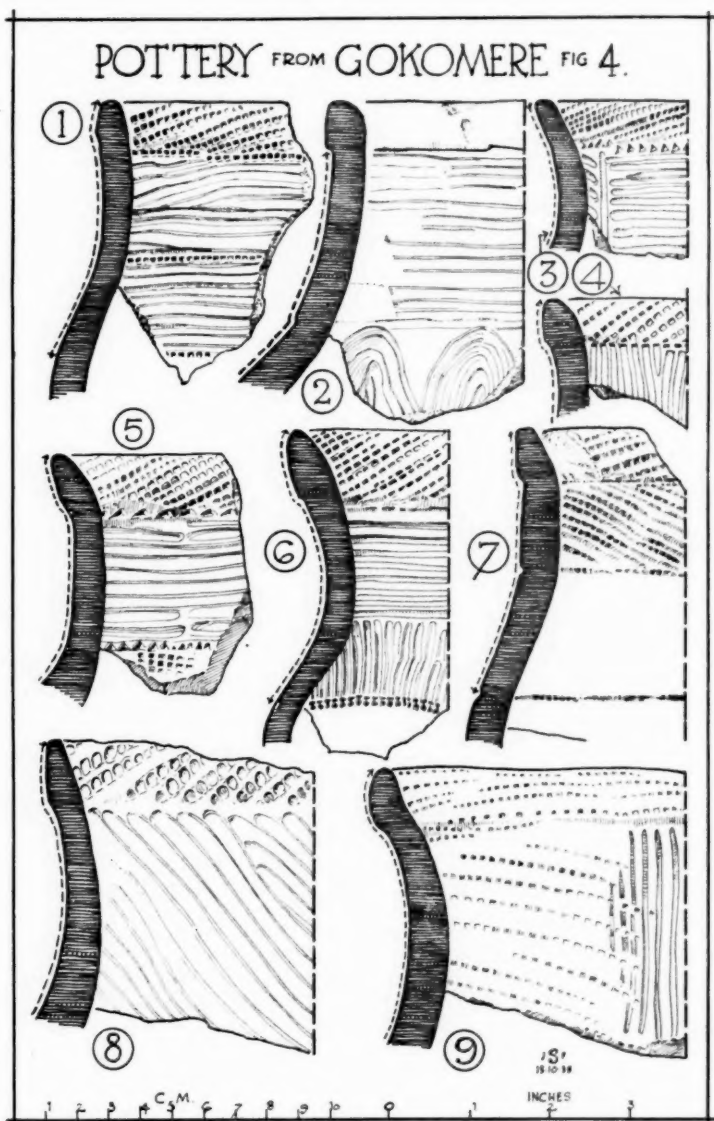
5. A shouldered pot or bowl, 9 inches over the rim, in a grey clay with a brown surface, matt externally and smoothed internally. The rim was rounded, the rim-band projected slightly and was decorated with diagonal comb-marks. The neck had a band 1½ inches in width, of lightly scraped lines between two lines of bold triangular impressions. Below this was another band of uncertain width, formed with irregular comb-marks. From Zone C, Tunnel Site. Class R₁.

6. A shouldered pot or bowl, 10 inches over the rim, in a grey clay with a purple surface, matt externally and smoothed internally. The rim was rounded and had a convex rim-band with diagonal comb-marks. Below this was another band of horizontal lines, and below this again was a band of vertical lines which had probably been made with a comb. This band was finished along its lower edge with a line of impressions made with a small stylus. From Zone C, Tunnel Site. Class R₁.

7. A shouldered pot or bowl, about 9 inches over the rim, in a gritty red clay with a pinkish surface, matt externally and smoothed internally. The rim was tapered on the inside, flattened and slightly rounded. The rim-band projected slightly and was decorated with roughly made diagonal comb-marks. Below this there was a wide band of similar comb-marks between two lines of the same. Below this again there was an undecorated band, which was terminated by a line of comb-marks along the shoulder of the pot. From Zone B, Tunnel Site. Class R₁.

8. A shouldered pot or bowl, about 8 inches over the rim, in a grey clay with a buff matt surface externally and a grey matt surface internally. The rim was tapered and flattened and had a vertical rim-band decorated with large comb-marks. Below this the neck was concave and was decorated with diagonally scraped lines. From the unstratified midden, Tunnel Site. Class R₁.

9. A shouldered pot or bowl, 10 inches over the rim, in a grey clay with a grey surface, matt externally and smoothed internally. The rim was rounded, tapered, and slightly hollowed internally. The rim-band had a convex section and was decorated with short



lengths of irregular horizontal comb-marks. The neck was concave and decorated in a similar manner, except that it appeared to have been divided into panels with roughly made horizontal lines. From the unstratified midden, Tunnel Site. Class R₁.

DESCRIPTION OF TEXT-FIGURE NO. 5.

1. A small shouldered pot, $4\frac{1}{2}$ inches over the rim, in a grey clay, finished matt externally and smoothed internally. The rim was flattened and had a slightly convex rim-band decorated with diagonal comb-marks. The neck was concave and decorated with square comb-marks grouped in vertical lines. From Zone B, Tunnel Site. Class R_1 .

2. A shouldered pot, 6 inches over the rim, in a grey clay, smoothed internally, with a light grey matt surface externally. The rim was finished square with a slightly projecting rim-band. The neck was decorated with square comb-marks arranged in vertical lines. From the unstratified midden, Tunnel Site. Class R_1 .

3. A shouldered pot, $6\frac{1}{2}$ inches over the rim, in a light grey clay, smoothed internally with a light buff matt surface externally. The rim was rounded and finished with a flattened roll which was decorated with diagonal comb-marks. Below this the neck was decorated with a band of herring-bone comb-marks between two lines of the same. These comb-marks are unusually fine. The interior surface shows a distinct rust mark. From the unstratified midden, Tunnel Site. Class R_1 .

4. A shouldered pot, 7 inches over the rim, in a brown clay with a black matt surface externally and a smoothed interior. The rim was tapered and rounded, and had a boldly projecting rim-band decorated with diagonal comb-marks. The shoulder had a line of comb-marks, and the neck was probably divided into panels which were alternately plain and decorated with fine comb-marks arranged in horizontal lines. From the unstratified midden, Tunnel Site. Class R_1 .

5. A pot or bowl with a vertical neck, about 10 inches over the rim, in a greyish-brown clay with a black surface, matt externally and smoothed internally. The rim was rounded and had a convex rim-band decorated with diagonal comb-marks. The neck was covered with fine comb-marks arranged vertically. The shoulder appears to have had a line of larger comb-marks. From the unstratified midden, Tunnel Site. Class R_1 .

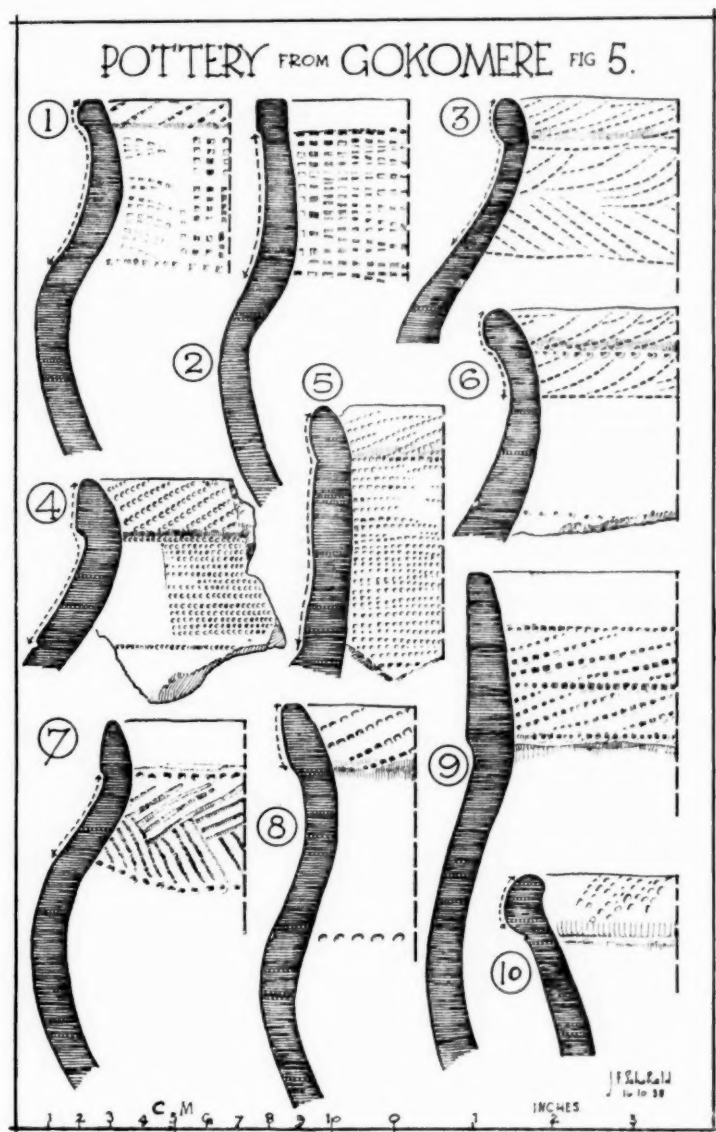
6. A shouldered pot or bowl, 11 inches over the rim, in a grey clay with a light buff surface, smooth internally and matt externally. The rim was rounded, with a convex rim-band decorated with diagonal comb-marks, below this there was a line of impressions made with a square stylus. The upper part of the neck had a band of diagonal comb-marks finished with a line of the same. On the shoulder there was a line of square impressions. This pot is very similar to No. 3. From the unstratified midden, Tunnel Site. Class R_1 .

7. A shouldered or bellied bowl, 11 inches over the rim, in a grey clay with a fine black burnished surface, except the decorated band which was matt. The rim was rounded and tapered and had a slightly projecting rim-band. Below this there was a wide band decorated with recessed lines in a rough alternate hatching, above and below this band were lines of square stylus impressions. All had been made on the wet clay. From Zone B, Tunnel Site. Class probably R_1 .

8. A shouldered bowl, $7\frac{1}{2}$ inches over the rim, in a reddish clay with a pinkish surface, with a matt finish externally and smoothed internally. The rim was flattened and rounded with a slightly convex rim-band decorated with diagonal comb-marks. The shoulder had a line of elliptical impressions. From the unstratified midden, Tunnel Site. Class R_1 .

9. A shouldered bowl, $9\frac{1}{2}$ inches over the rim, in a grey clay with a grey smoothed interior and a reddish matt exterior. The rim was rounded, the projecting rim-band was 2 inches in width, and was decorated with a double band of comb-marks with three lines of the same. From the unstratified midden, Tunnel Site. Class R_1 .

10. A fragment, probably from the rim of a large beaker bowl, about 11 inches over the rim, in a grey clay, finished externally with a smooth surface and internally with a black burnish. The rim was slightly tapered, rounded and introverted, externally it



had a bold ovolo finished with a well-defined quirk, and was decorated with six lines of diagonal comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

DESCRIPTION OF TEXT-FIGURE NO. 6.

1. A deep bowl, 9 inches over the rim, in a grey clay, with a black matt surface externally and a smoothed finish internally. The rim was rounded, and just below it was an irregular band, formed with rough diagonal incisions between two lines of comb-marks. From Zone C, Tunnel Site. Class R₁.

2. A deep bowl, 6 inches over the rim, in a grey clay with a light buff smoothed surface. The rim was rounded, and just below it were three lines of rough comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

3. A bowl with a contracted opening, or neckless pot, 8 inches over the rim, in a grey clay with a matt surface. The rim was rounded and introverted, with a slight hollow below it internally. Seven-eighths of an inch below the rim externally there was a band formed with bold diagonal comb-marks between two lines of the same. From the unstratified midden, Tunnel Site. Class R₁.

4. A bowl, or neckless pot, probably spherical, with a contracted opening, 9 inches over the rim, in a grey clay with a matt surface, black inside and grey outside. The rim was rounded on the inside and tapered to a ridge, the rim-band was slightly convex; below it was a wide band of diagonal comb-marks between two recessed lines of the same, whilst another similar line divided the band horizontally. From the unstratified midden, Tunnel Site. Class R₁.

5. Probably a fragment of a spherical pot, about 11 inches over the rim, in a blackish clay with a black burnished surface which shows traces of graphite. The rim was rounded, and the convex rim-band projected slightly; below this there was a slightly bulging band, 1½ inches in width, decorated with roughly made comb-marks in herring-bone between two recessed lines of the same. From Zone C, Tunnel Site. Class R₁.

6. A deep bowl, about 10 inches over the rim, in a gritty grey clay with a matt surface. The rim was tapered and rounded, the rim-band was convex; below it there was a wide bulging band of diagonal comb-marks between two recessed lines of the same. From Zone A, Tunnel Site. Class R₁.

7. A pot or bowl with a constricted neck, about 9 inches over the rim, in a dark brown ware with a smooth surface. The rim was rounded, and below it there was a band composed of four lines of irregular comb-marks. From Zone A, Tunnel Site. Class R₁.

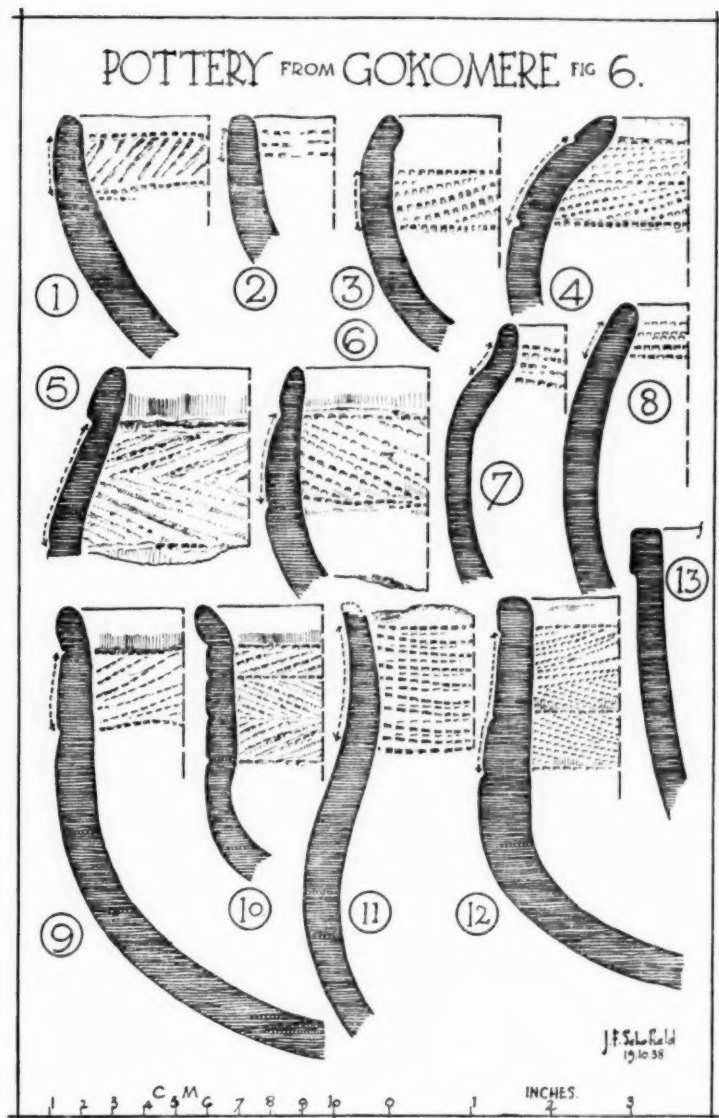
8. A bowl with a constricted opening, 10½ inches over the rim, in a grey clay partially burnt to a light red, and finished with a grey matt surface. The rim was rounded, and directly below it was a band of four or five lines of comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

9. A deep, or beaker bowl, 11 inches over the rim, in a grey clay. The rim-band externally and the upper part of the interior had a black burnish, the remainder was finished to a blackish matt. The rim was rounded, the rim-band was slightly convex, directly below it there was an irregular band of diagonal comb-marks between two recessed lines of the same. From Zone C, Tunnel Site. Class R₁.

10. A deep, or beaker bowl, 6 inches over the rim, in a black clay with a black burnish, excepting the decoration which was matt. The rim was rounded and slightly everted, the rim-band was convex. Directly below it was a band composed of three ribs decorated with alternating diagonal comb-marks, which were outlined with recessed lines of the same. From Zone A, Tunnel Site. Class R₁.

11. A shouldered pot, 6 inches over the rim, in a grey clay with a matt surface. The rim is much worn, but seems to have been rounded and slightly everted. The neck was slightly concave and decorated with panels of comb-marks in horizontal lines. From Zone C, Tunnel Site. Class R₁.

12. A deep, or beaker bowl, 5 inches over the rim, in a grey clay with a matt surface externally and a rough finish internally. The rim was flattened, and the rim-band had a slight projection. Below it there was a wide band composed of two convex ribs,



decorated with fine comb-marks. These ribs were outlined with recessed lines of comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

13. A deep bowl, 6 inches over the rim, in a grey clay, with a grey burnish internally and a brindled matt finish externally. The rim was flattened and had a rim-band with a slight projection. From the unstratified midden, Tunnel Site. Class R₁.

DESCRIPTION OF TEXT-FIGURE NO. 7.

1. A bowl, $5\frac{1}{2}$ inches over the rim, with a height of $3\frac{1}{2}$ inches, in a coarse grey clay, with a greyish-buff matt surface externally and left rough internally. The rim was folded over to form a bevelled surface to the outside. This bevel had at least two spout-like grooves formed in it. Below the rim a narrow concave neck was formed and was decorated with three lines of comb-marks and round impressions. The junction of the neck with the body was marked with a distinct ridge or carination. The body was decorated with festoons formed with lines of comb-marks. The festoon which came below the spouts appears to have had a central feature which was absent from the other festoon. From Zone B, Tunnel Site. Class uncertain.

2. A small shouldered pot, $3\frac{1}{2}$ inches over the rim, with a height of 4 inches, in a fine grey clay, with a black burnish externally and a matt finish internally. The rim was rounded and slightly everted. The neck was concave, and its junction with the body was covered with a narrow band of roughly made diagonal incisions. Spaced equidistantly below this band were three motifs, each of which were formed by pressing two fingers into the wet clay of the body in an upward direction, and thus forming shallow grooves. The junction of these grooves with the band was covered with three small pellets of clay. From a depth of about 15 inches below the surface, Cave Site. Class R_{3a}.

3. A fragment of a shouldered pot, about 6 inches over the rim, in a grey clay, with a deep brown crackled matt surface. The rim was rounded and slightly everted, the neck was concave and the shoulder was decorated with a line of triangular impressions. From a depth of 11 feet at the Dam. Class uncertain.

4. A fragment of a carinated pot or bowl, about 8 inches in diameter, in a grey clay, smooth internally with a deep brown matt finish externally. The carination had, on its upper aspect, a band of fine diagonal comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

5. A shallow bowl, $4\frac{1}{2}$ inches in diameter, with a height of $2\frac{1}{2}$ inches, in a gritty grey clay with a smooth surface. The rim was rounded and bevelled to the inside. Below the rim externally there was a deep horizontal line. From Zone B, Tunnel Site. Probably Class R₁.

6. A deep bowl, about 9 inches over the rim, in a gritty grey clay; the rim was finished matt and the remainder of the surface was smoothed. The rim was rounded with a slight introversion, the upper surface was flattened and fluted with shallow grooves as if made by drawing the fingers over it. The upper surface was also decorated with lines of diagonal comb-marks. The rim-band was convex, and below it there was a band of diagonal comb-marks between two recessed lines of the same. From Zone B, Tunnel Site. Class R₁.

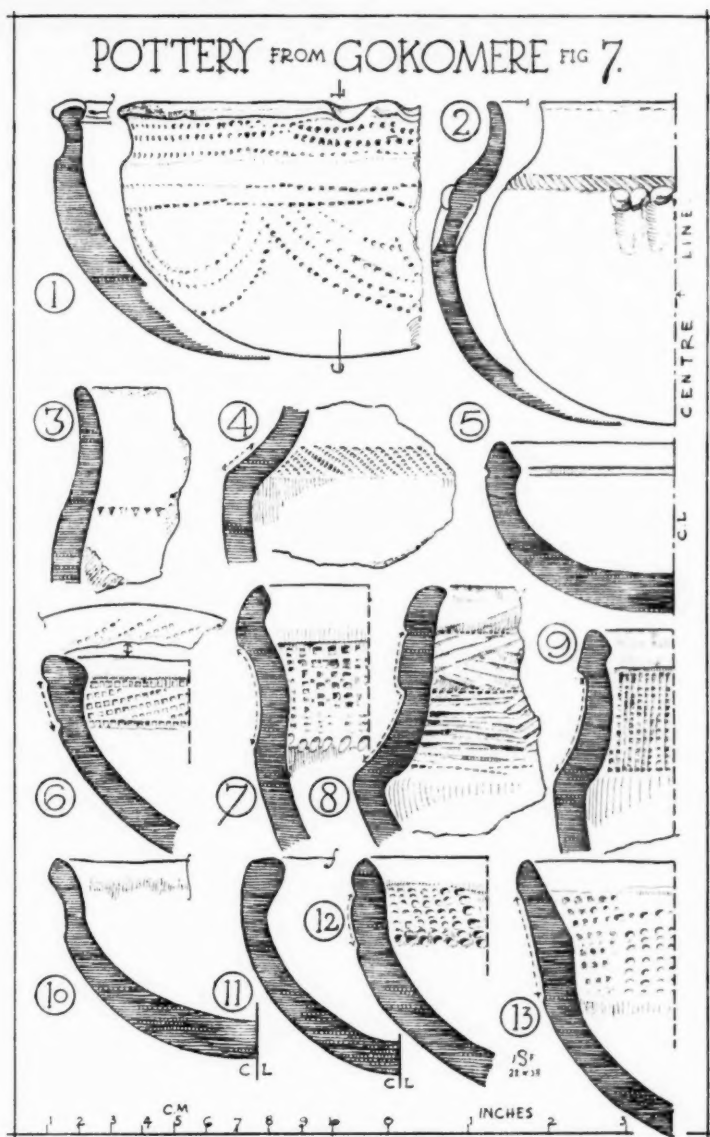
7. A carinated bowl, about 7 inches over the rim, in a grey clay, with a matt surface externally and a black burnish internally. The rim was tapered, rounded and introverted, with a bold ovolo, finished with a distinct quirk externally. The neck was slightly concave and joined the body with a slight carination. It was decorated with large square comb-marks in parallel lines. There was a line of irregular oval impressions along the ridge of the carination. From the unstratified midden, Tunnel Site. Class R₁.

8. A carinated bowl, about $9\frac{1}{2}$ inches over the rim, in a grey clay, finished matt, with the exception of the rim and the upper part of the interior which were burnished. The rim was rounded and slightly introverted; externally it had a bold ovolo section. Below it there was a bulging rib of diagonal counter-hatching between two recessed lines of comb-marks. The neck was concave with wide irregular horizontal lines. Just above the carination there was a line of comb-marks. From Zone C, Tunnel Site. Class R₁.

9. A carinated bowl, about 10 inches over the rim, in a buff clay with a purple grey burnish. The rim was bevelled internally with a slight projection, externally it had a flat projecting rim-band. The neck was concave, decorated with vertical dragged comb lines, and joined the body with a slight carination. From the unstratified midden, Tunnel Site. Class R₁.

10. A small bowl, $5\frac{1}{2}$ inches over the rim, with a height of $2\frac{1}{2}$ inches, in a coarse grey clay with a rough surface. The rim was tapered to a rounded ridge and had a convex projection on the outside. Below this the neck was slightly concave and joined the body with a rounded ridge or sub-carination. From Zone B, Tunnel Site. Class R₁.

11. A small bowl, 4 inches over the rim, with a height of $2\frac{1}{2}$ inches, in a coarse grey



clay with a rough surface. The rim was flattened and rounded with a convex projection on the inside. From the unstratified midden, Tunnel Site. Class R₁.

12. A deep bowl, 6½ inches over the rim, in a gritty grey clay with a matt surface. The rim was brought to a ridge and had a convex rim-band, below this there was an irregular band of comb- and/or bead-marks. From Zone C, Tunnel Site. Class R₁.

13. A deep bowl, 6 inches over the rim, in a gritty grey clay, with a matt surface externally and a black burnish internally. The rim had a steep bevel internally, and was brought to a ridge with a convex rim-band. Below this the neck was slightly concave and decorated with irregular vertical lines of comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

DESCRIPTION OF TEXT-FIGURE NO. 8.

1. A shouldered bowl, 7 inches over the rim, in a grey clay with a matt finish. The rim was brought to a ridge and had a convex rim-band which was separated from the neck by a recessed line of comb-marks; a similar line marked the junction of the neck and the body. From the unstratified midden, Tunnel Site. Class R₁.

2. A carinated bowl, 9 inches over the rim, in a grey clay; the interior and the rim-band had a brindled burnish, and the remainder a matt buff finish. The rim was rounded and everted with a convex rim-band, which was separated from the neck by a line of narrow comb-marks. The neck joined the body with a slight carination, and directly above this it was decorated with a band of counter-hatched diagonal comb-marks similar to the above. From Zone C, Tunnel Site. Class R₁.

3. A shouldered bowl, 11 inches over the rim, in a grey clay; the rim-band and the interior were burnished grey, and the remainder had a buff matt finish. The rim was rounded and everted with a convex rim-band. The neck was concave and decorated with a double band of diagonal comb-marks. Similar to fig. 5, 3 and 6, and to 1 and 2 above. From the unstratified midden, Tunnel Site. Class R₁.

4. A shouldered bowl, 5½ inches over the rim, with a height of 3½ inches, in a grey clay, with a black burnish externally and a rough surface internally. The rim was tapered to a ridge and had a convex rim-band, below which there was a band of diagonal comb-marks between two lines of the same. The neck joined the body with a rounded angle or sub-carination. From the unstratified midden, Tunnel Site. Class R₁.

5. A shouldered bowl, 9 inches over the rim, in a black clay, with a graphite burnish internally and over the rim-band, the remainder being finished with a black matt surface. The rim was flattened and rounded with a vertical rim-band. Below this the neck bulged outwards and was decorated with a band of diagonal incised lines between two lines of comb-marks. From the unstratified midden, Tunnel Site. Class R₁.

6. A bowl, 7 inches over the rim, in a gritty grey clay, finished with a black burnish internally and over the rim-band, the remainder being finished with a grey matt surface. The rim was tapered and rounded with a vertical rim-band. Below this the neck bulged outwards and was decorated with herring-bone comb-marks, arranged in alternating directions. From the unstratified midden, Tunnel Site. Class R₁.

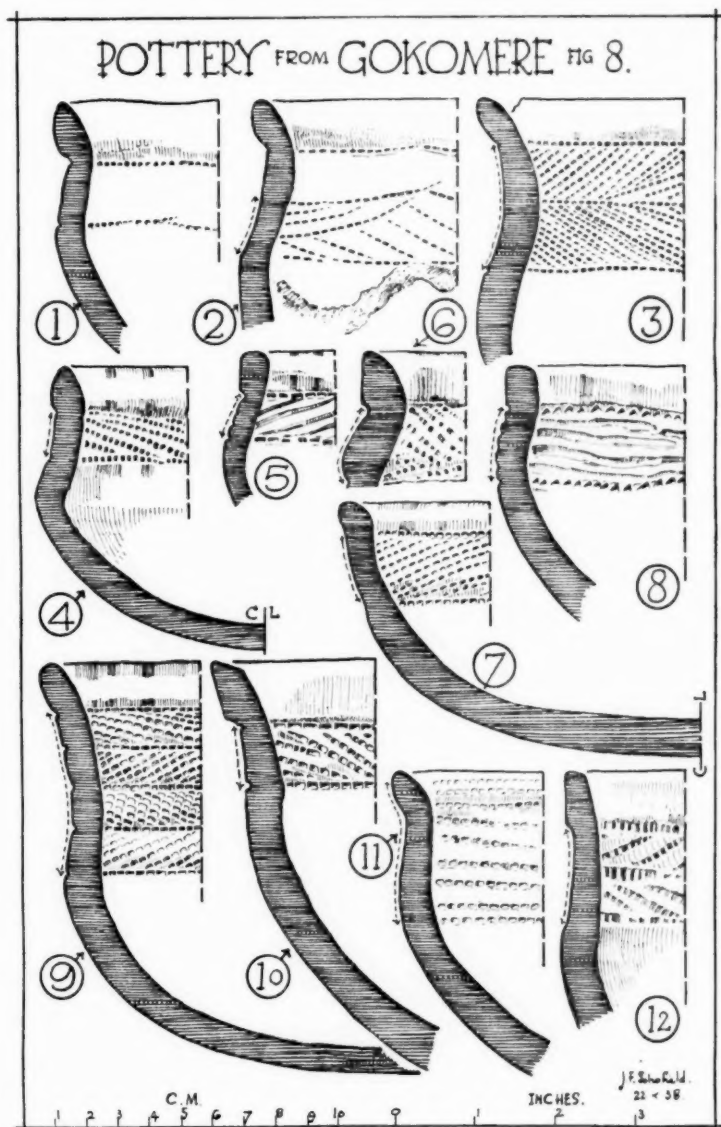
7. A shallow bowl, 9 inches over the rim, with a height of 3½ inches, in a gritty grey clay, with a black burnish internally and over the rim-band, the remainder being finished to a black matt surface. The rim was rounded and the rim-band was slightly convex. Below it there was a recessed convex band of diagonal comb-marks between two lines of the same. From Zone B, Tunnel Site. Class R₁.

8. A deep bowl, about 9 inches over the rim, in a grey clay; the interior was burnished with graphite, the rim had a black burnish, and the remainder appears to have had a black matt surface. The rim was rounded and flattened and had a vertical rim-band, the lower edge of which was irregular. Below this there was a slightly bulging band of wide lines between two lines of triangular impressions. From Zone B, Tunnel Site. Class R₁.

9. A beaker bowl, 10 inches over the rim, with a height of 5 inches, in a grey clay; the interior and the rim-band were burnished black and the remainder finished to a grey matt surface. The rim was rounded and everted, the rim-band was convex, and below it there was a wide fourfold band of alternating diagonal comb-marks with recessed lines of comb-marks between each of the ribs. From the unstratified midden, Tunnel Site. Class R₁.

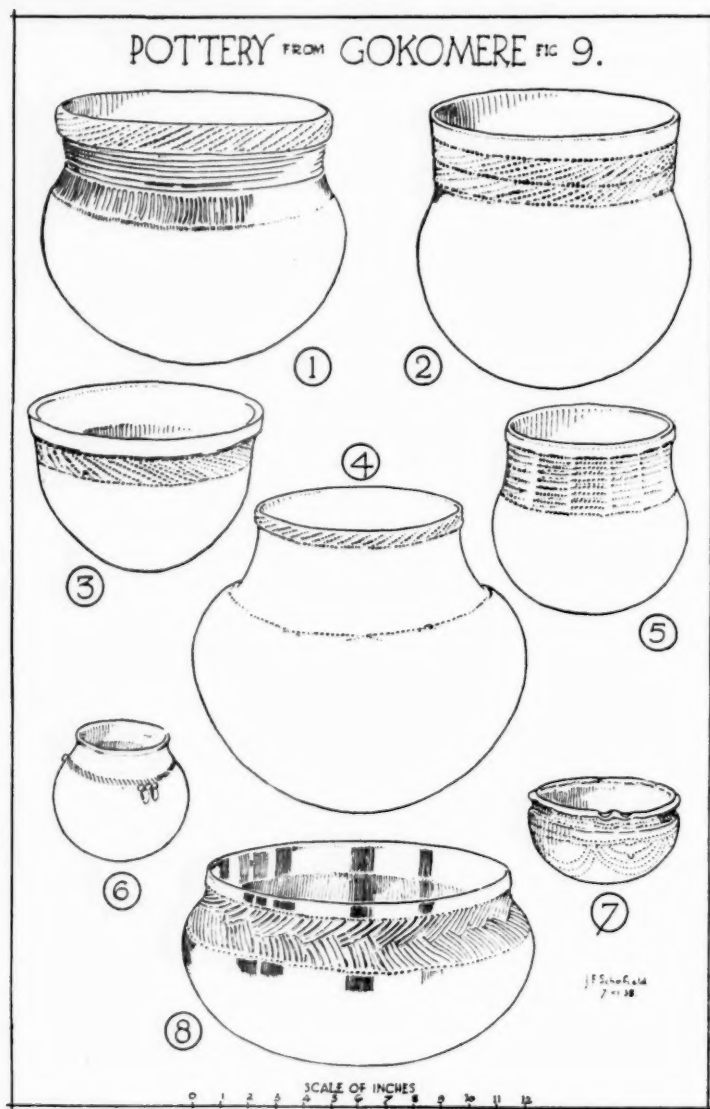
10. A basin-shaped bowl, 8½ inches over the rim, in a grey clay; the rim-band and the upper part of the interior had a grey burnish and the remainder was finished to a grey matt surface. The neck and the rim-band were everted, and the rim was bevelled inwards. Below the rim-band there was a band of diagonal comb-marks between two recessed lines of the same. From Zone B, Tunnel Site. Class R₁.

11. A basin-shaped bowl, about 10½ inches over the rim, in a coarse grey clay with a smooth greyish surface. The rim was rounded and everted. Both the neck and the



upper part of the body were decorated with horizontal lines of roughly made comb-marks. From Zone A, Tunnel Site. Class R₁.

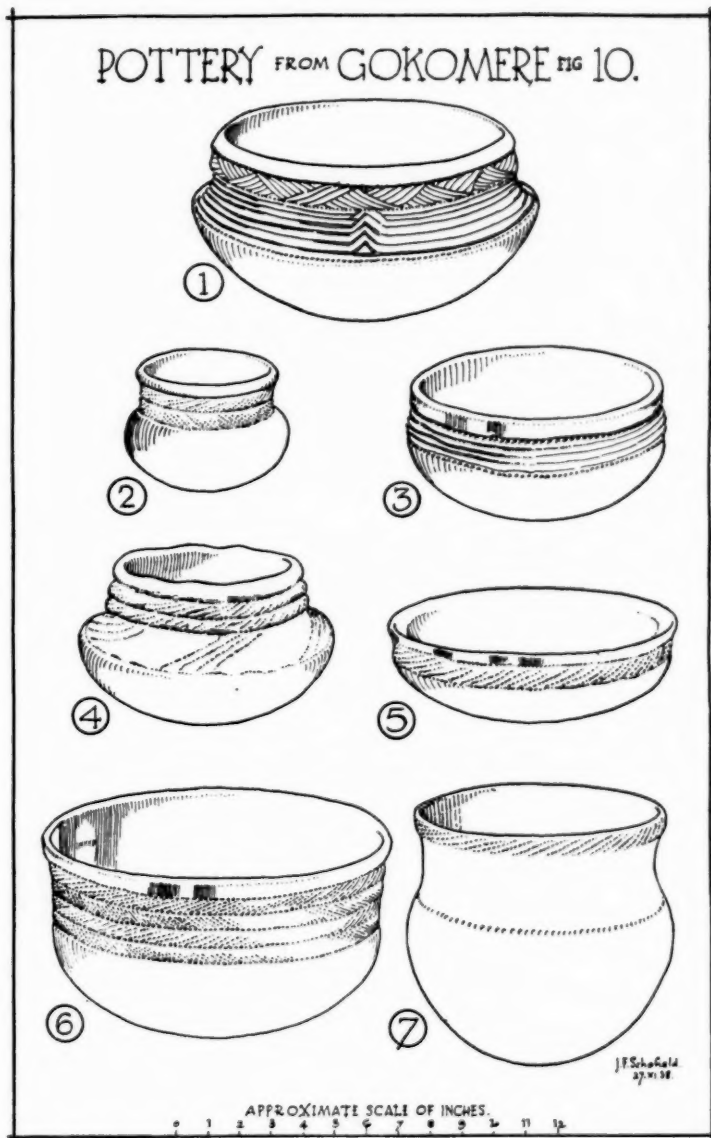
12. A deep bowl, 9 inches over the rim, in a gritty grey clay with a greyish brown burnished surface. The rim was rounded and flattened and had a vertical rim-band; below this there was a recessed and slightly concave double band, decorated with alternating diagonal comb-marks separated by horizontal lines of the same. From Zone C, Tunnel Site. Class R₁.



DESCRIPTION OF TEXT-FIGURE No. 9.

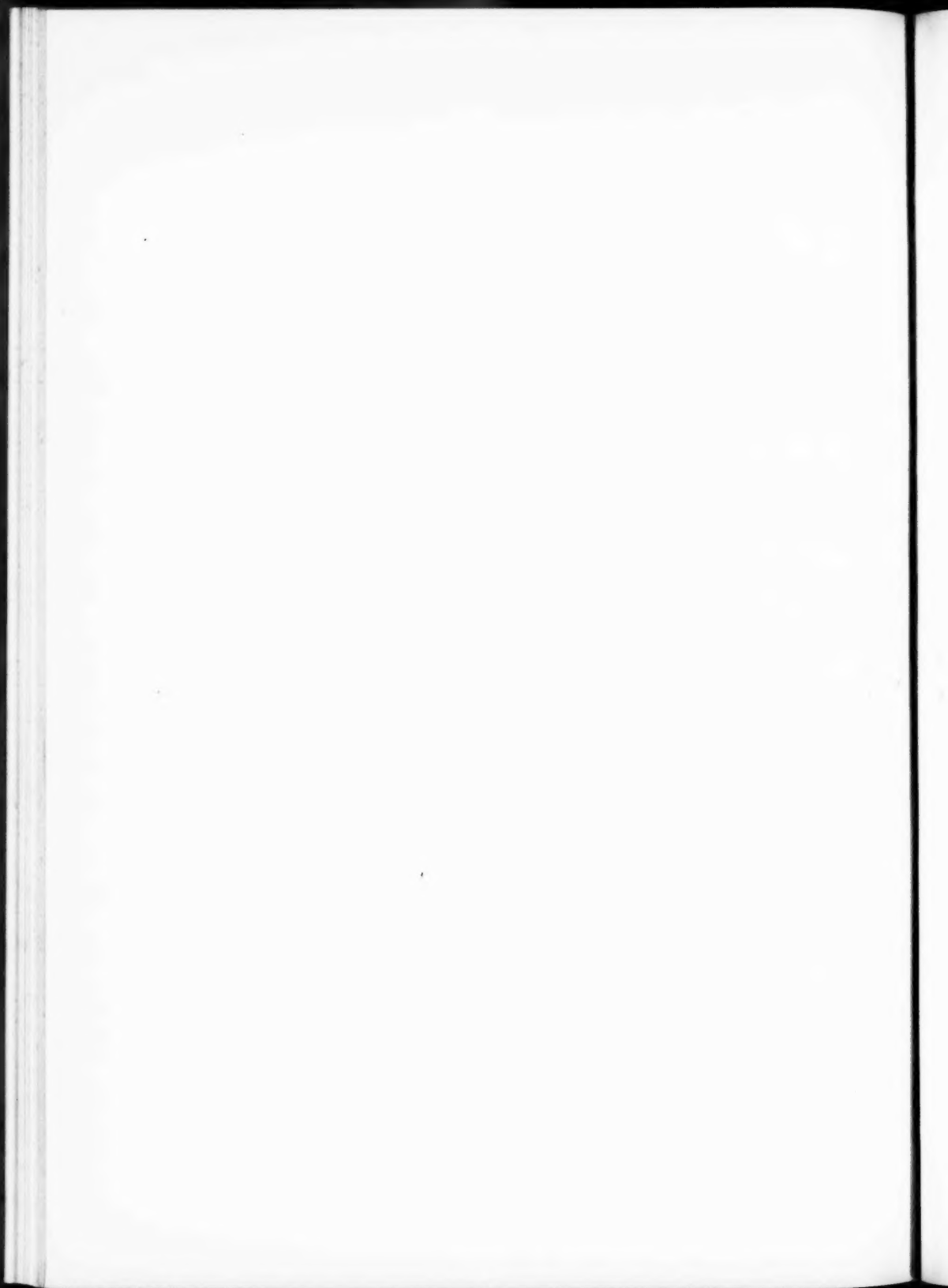
- | | |
|-------------------------------|------------------------------|
| 1. See Text-figure No. 4, 6. | 5. See Text-figure No. 5, 2. |
| 2. See Text-figure No. 5, 9. | 6. See Text-figure No. 6, 1. |
| 3. See Text-figure No. 8, 10. | 7. See Text-figure No. 6, 2. |
| 4. See Text-figure No. 2, 6. | 8. See Text-figure No. 5, 7. |

POTTERY FROM GOKOMERE FIG 10.



DESCRIPTION OF TEXT-FIGURE No. 10.

- | | |
|------------------------------|------------------------------|
| 1. See Text-figure No. 7, 8. | 5. See Text-figure No. 8, 7. |
| 2. See Text-figure No. 3, 7. | 6. See Text-figure No. 8, 9. |
| 3. See Text-figure No. 8, 8. | 7. See Text-figure No. 5, 8. |
| 4. See Text-figure No. 3, 6. | |



A PRELIMINARY INVESTIGATION OF THE IMPORTANCE OF
DESICCATION, TEMPERATURE, AND SALINITY AS FACTORS
CONTROLLING THE VERTICAL DISTRIBUTION OF CERTAIN
INTERTIDAL MARINE GASTROPODS IN FALSE BAY, SOUTH
AFRICA.

By G. J. BROEKHUYSEN, Ph.D.,

Department of Zoology, University of Cape Town.

(With Plates LII and LIII, and six Text-figures.)

(Read April 19, 1939. Revised MS. received November 15, 1939.)

CONTENTS.

	PAGE		PAGE
INTRODUCTION	255	SALINITY	278
DESICCATION	256	SUMMARY	289
TEMPERATURE	269	REFERENCES	291

INTRODUCTION.

The vertical distribution of the Prosobranchs *Littorina knysnaënsis* Philippi, *Thais dubia* (Krauss), *Oxysteles variegata* (Anton), *Oxysteles tigrina* (Dillwyn), *Oxysteles sinensis* (Gmelin), *Cominella cincta* (Röding), and *Turbo sarmaticus* Linn. has recently been worked out by Bokenham and Neugebauer (1938), who carried out their observations at St. James and Simonstown on the False Bay coast. It was shown by these authors that the species enumerated are distributed in overlapping zones on the shore (fig. 1). Observations made in the course of the present work confirm these findings in a general way, except that, as mentioned in the footnote on p. 128 of the paper referred to, it is the present author's opinion that *T. dubia* extends somewhat higher up than *O. variegata*. The zonation, however, has in the main been taken for granted.

The present investigation was started with the aim of studying the factors which are responsible for the typical distribution in zones shown by the species considered. Such an investigation may be expected to be a complicated one, as many factors may be involved and interaction among them is very likely to occur. This probably is the reason why such an investigation has never been carried out. It is the aim of the present

author to attempt to solve the problem in a series of papers of which this is the first. The object of the present investigation was to study the importance of certain factors which appear to be immediately connected with the upper limits of the observed zonation, and to obtain a basis for further investigation. The action of three environmental factors, *i.e.* desiccation, temperature, and salinity, upon mature individuals of the several species was studied. All the material used was collected on the False Bay coast at Strandfontein and St. James (fig. 2). On account of the difficulty of getting enough material of *Turbo sarmaticus* for the experimental work, this species was omitted.

DESICCATION.

Introduction.—Although the importance of desiccation as a leading factor controlling the distribution of intertidal organisms is generally accepted, it has never actually been proved. Most of the investigations which have been conducted have been concerned primarily with the determination of average times of exposure for organisms inhabiting different levels (Huntsman, 1918; Colman, 1933; Moore, 1936; Grubb, 1936; Hewatt, 1937; Bokenham, Neugebauer and Stephenson, 1938, etc.). Ferronnière (1901), working with worms, showed that organisms from higher levels withstood desiccation better than those from lower levels. Baker (1909, 1910) in her experimental work on certain intertidal algae, in which the several species were reared under different conditions of periodic desiccation, and in which the effect of this factor on germination was studied, came to the conclusion that "in the lowest zones the primary factor is probably rate of growth," and that "in the upper zones the determining factor is tolerance of desiccation." A few authors, working on the zonation of intertidal algae, have obtained data on the rate of water-loss in relation to intertidal position (Isaac, 1933, 1935; Zaneveld, 1937). Zaneveld has gone still further and has attempted to explain the mechanism by which some species can regulate their water-loss. But even in these cases it has not been directly proved that degree of desiccation is responsible for the level on the shore inhabited by an organism, although considerable weight has been given to this view. A comparison between the lethal water-loss and the average, or perhaps better the maximal, water-loss sustained under natural conditions is still required.

In the case of the six gastropods dealt with in this paper the influence of desiccation as a controlling factor in the vertical distribution has been studied, and special attention has been paid to (a) the desiccation-resisting capacity, (b) the rate of desiccation, and (c) the desiccation under natural conditions.

The Desiccation-resisting Capacity of the Several Species.—To obtain

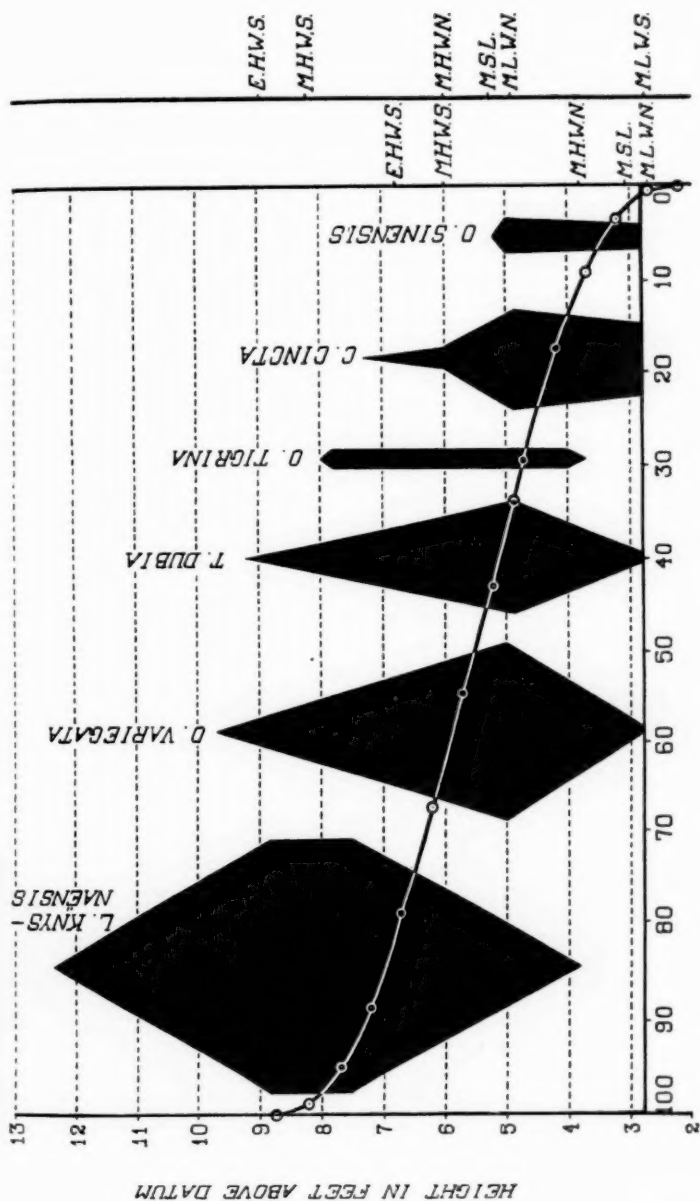


FIG. 1.—The vertical distribution of *Littorina knysnaensis*, *Oryzetele tigrina*, *Thais dubia*, *Oryzetele sinensis*, and *Oryzetele cincta*, in relation to tide-levels. Two series of tide-levels are inserted, the lower ones representing levels calculated from tide-gauge records, the upper ones being raised 2.2 feet above the lower ones, to allow for the wash-zone. The abbreviations refer to extreme and mean high and low waters of spring and neap tides respectively (e.g. E.H.W.S.=extreme high water of springs). Superimposed upon this figure is a curve, calculated from tide-gauge records, showing percentage exposure at the various levels.

This curve is related to the upper series of tide-levels. (From Bokenham and Neugebauer, 1938.)

data on the resistance to water-loss, the following experiments were carried out. A number of snails * (in most cases kept in the laboratory for a day) were dried with blotting-paper and subsequently placed in small petri-dishes of known weight. The wet weight of the snails was then determined by weighing the dishes containing them. After having been weighed, the dishes were put into an incubator in which the snails were dried above calcium chloride. At intervals a dish was taken out and the loss of water estimated by weighing the dish, after which the snails were submerged for some time in sea-water and the number of snails still living was recorded. A snail was considered to be alive when some response was shown to mechanical agitation. Two series of observations were carried out. In the first the incubator had been switched off and the snails were therefore subjected to room temperature, in the second the incubator had been switched on and the temperature to which the snails were subjected was 39 to 40° C. The results of these experiments are recorded in Table I, and are graphically expressed in figs. 3A and 3B.

TABLE I.
Experiments on Desiccation-resisting Capacity at Room Temperature
(± 14 to $\pm 27^\circ$ C.) and at ± 39 to $\pm 40^\circ$ C.

Species.	Minimum percentage of water-loss at which death occurred.		Minimum percentage of water-loss at which practically all were dead.	
	At room temperature.	At 39 to 40° C.	At room temperature.	At 39 to 40° C.
<i>O. sinensis</i> . . .	3	3	9	9
<i>O. tigrina</i> . . .	7	4	11-12	7
<i>C. cincta</i> . . .	10	8	13	11
<i>O. variegata</i> . . .	12	10	21	16
<i>T. dubia</i> . . .	15	13	24	20
<i>L. knysnaënsis</i> . .	15	14	29	25-26

This table shows that the values obtained at 39 to 40° C. are lower on the whole than those obtained at room temperature. This would

* In the experiment at room temperature the numbers per dish were: *L. knysnaënsis* 49-51, *T. dubia* 20-25, *O. variegata* 20-22, *C. cincta* 14-16, *O. tigrina* 11-16, *O. sinensis* 12-16.

The figures for the experiment at a temperature of 39 to 40° C. were as follows: *L. knysnaënsis* 99-103, *T. dubia* 20-31, *O. variegata* 18-21, *C. cincta* 12-19, *O. tigrina* 10-16, *O. sinensis* 13-23.

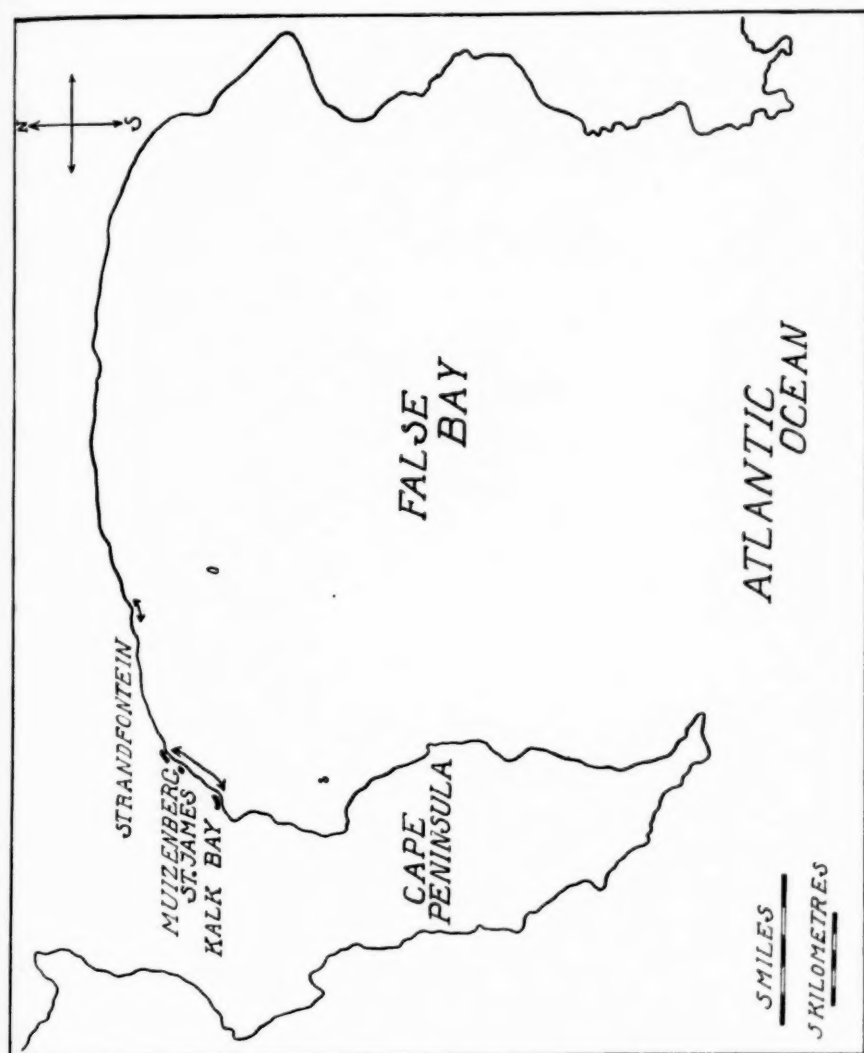


FIG. 2.—Map of the Cape Peninsula and False Bay, showing the localities mentioned in this paper.
(Based on part of Admiralty Chart No. 2082, 1914 edition.)

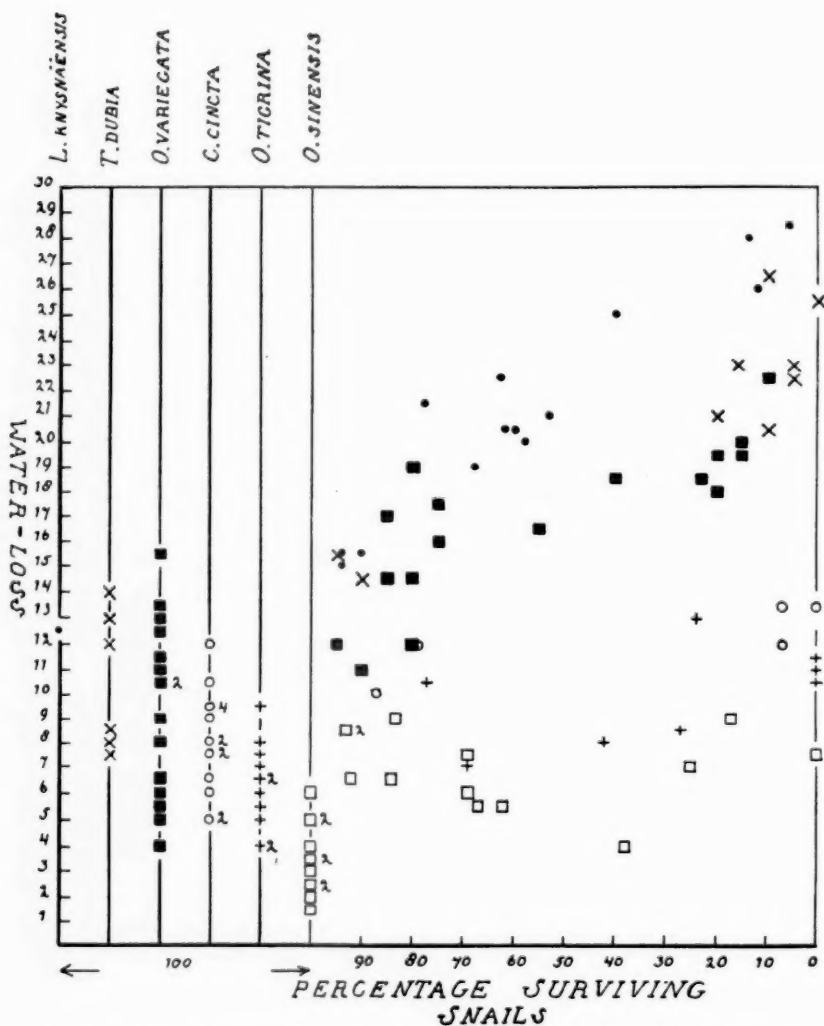


FIG. 3A.—Lethal water-loss values at room-temperature. The water-loss is given as percentages of the wet weight of the snails at the beginning of the experiment. The ordinate representing 100 per cent. surviving snails has been repeated six times, once for each of the species, to avoid confusion.

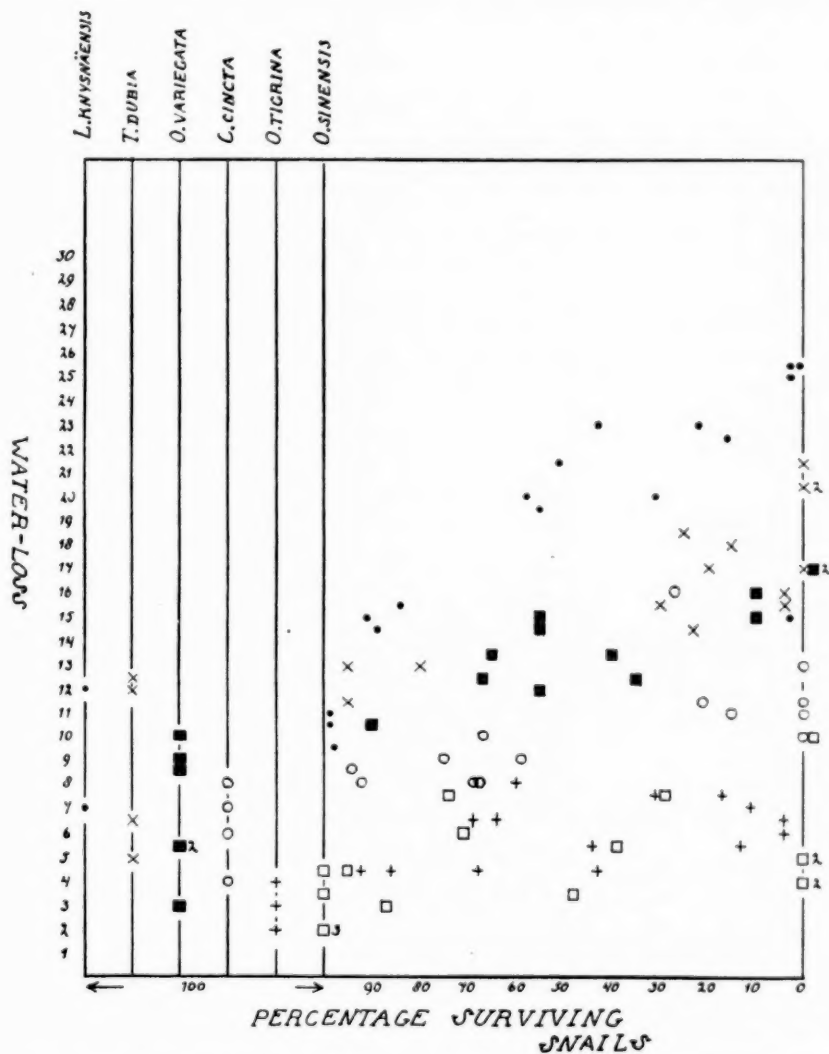


FIG. 3B.—Lethal water-loss values at a temperature of 39 to 40° C. See also explanation of fig. 3A.

indicate that high temperatures weaken the resistance to desiccation. As, however, 39 to 40° C. appears to be close to the lethal temperature for *O. sinensis*, *O. tigrina*, and *C. cincta* when kept submerged (p. 270), too great a value should not be attached to the results obtained at high temperatures for these species.

The table and figures reveal that the several species show differences in the amount of water which can be lost before death occurs, and can therefore be arranged in a sequence according to the amount of water-loss which is lethal. If this order be compared with their order of distribution on the shore as shown by fig. 1, it becomes clear that there is a considerable correspondence between the two, the species which occur lower down in the intertidal belt being more sensitive to desiccation than those at higher levels. *O. tigrina* presents the only marked exception. Although this species inhabits fairly high levels, it is most commonly confined to pools or damp places, and for this reason is probably less exposed to desiccation than a form inhabiting open rock at similar levels. Further, it was found that individual variation, as shown in the difference between the amount of water-loss which is fatal to some individuals of a species and the amount which kills nearly all of them, is greatest for the species with the higher resistance to desiccation.

The Rate of Desiccation.—In order to obtain comparable data relating to the several species, the following experiment was carried out.

Several large petri-dishes containing calcium chloride were put on the floor of an incubator, the openings in which had been closed, thus preventing ventilation. Small dishes, each containing a number of snails of one species which had been previously dried with blotting-paper, were kept on a gauze tray above the calcium chloride. At intervals the dishes were weighed and the loss of water estimated. Two series of observations were carried out in this way. In the first series, two dishes of *L. knysnaënsis* were included. One of these contained individuals which had been killed by pouring hot water over them, and whose bodies were thus not completely shut up in the shells by the closing of the operculum. Those in the other dish, though alive, had had their vitality much reduced by being kept for some time in the laboratory. The individuals of the other five species were all in a healthy condition. The second series consisted of six dishes, one of each of the species, and in this case all the specimens, including those of *L. knysnaënsis*, were in a healthy condition. Both series of observations were carried out at room temperature. The water-loss was calculated as a percentage both of the original wet weight of the snails and of the dry weight at the end of the experiment. To obtain this dry weight the snails were dried at a temperature of over 100° C.

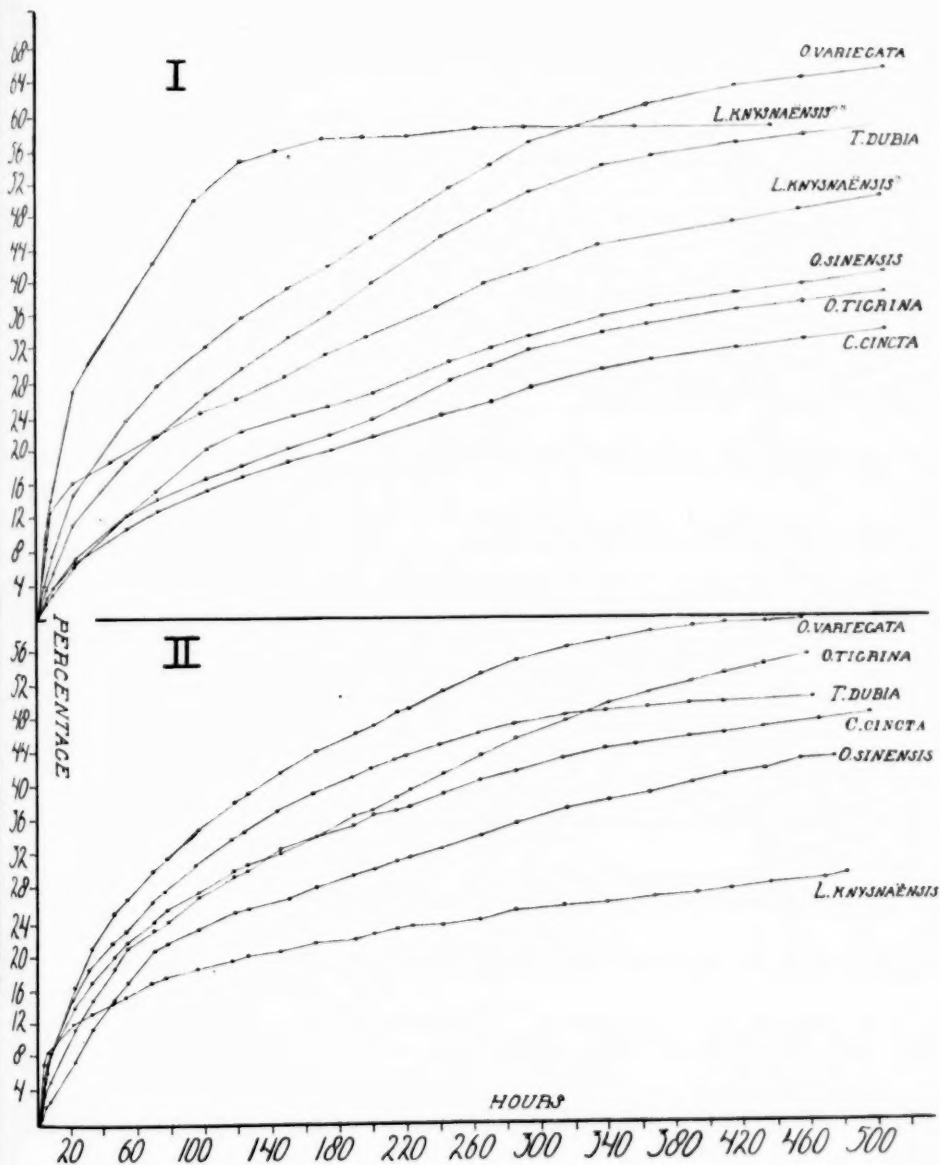


FIG. 4.—The rate of water-loss of the several species. The ordinates represent the water-loss expressed as percentages of the dry weight of the snails at the end of the experiment, while the abscissae represent the duration of desiccation in hours. * means that the vitality of the individuals concerned had been lowered, ** means that the individuals concerned had been killed by pouring hot water over them.

The results are recorded in fig. 4. In this figure the water-loss is given as percentages of the dry weight, as this was thought to be the more accurate one, and as no essential difference was found between the curves obtained on a wet-weight basis and those on a dry-weight basis.

This figure shows that individuals of *L. knysnaënsis* in a healthy condition lose water fairly rapidly until about 9 per cent. of the dry weight (about 7 per cent. of the wet weight) of the snail has been lost. After this there is a sudden marked reduction in the water-loss, as indicated by the horizontal character of the curve. The fact that in the case of snails which have lost their vitality this reduction occurs after a much higher percentage of water has been lost, and that in the case of the dead snails it fails to occur (or rather, occurs only when the tissues of the snails have lost as much water as they will lose at room temperature), makes it probable that in this species the opercular mechanism, together with the low degree of porosity of the shell, provide efficient protection against excessive desiccation. In the other species no such sudden change in rate of water-loss was found.

Except in the case of *L. knysnaënsis*, there is little relationship between rate of loss of water under these conditions and the zonal distribution on the shore. In fact *O. variegata*, which lost water most rapidly in both series of experiments, is the one of which the bulk of individuals, after *L. knysnaënsis*, is most exposed to desiccation on the shore. The reverse is true of *O. sinensis* and *C. cincta*.

It thus appears that *L. knysnaënsis* is very efficiently protected against desiccation. In the first place it can withstand a water-loss of over 14 per cent. of its fresh weight without serious injury, and in the second place it can decrease the rate of water-loss efficiently, which is probably done by contracting and closing of the entrance of the shell with the operculum. The ability of this species to inhabit the highest intertidal levels is dependent upon these protective mechanisms, so far as desiccation is concerned. The intertidal positions of the other species show a definite connection with the amount of water-loss they are able to endure, but little with the rate at which water is lost.

We may postulate the existence among intertidal snails of three types, distinguished by the way in which the structure or behaviour of the animal affects the water-loss during desiccation.

- (a) The operculum is closed and but little further water is lost.
- (b) The shell entrance remains open and the water-loss is continuous.
- (c) The operculum is closed, but the water-loss remains more or less continuous as the shell is so porous, or the operculum fits so badly, that closing of the operculum does not affect the rate of water-loss efficiently.

L. knysnaënsis apparently belongs to the first type,* while the other species fall under the second and third types.

Desiccation under Natural Conditions.—In order to discover to what extent degree of desiccation may be responsible for the zonal distribution of the species under consideration, it was necessary to determine the times of exposure which become harmful to them in their natural habitats, and to compare these figures with the times of exposure which the majority of the individuals of the several species actually experience on the seashore.

The following experiment was therefore carried out to estimate the water-loss suffered by the snails of each species under somewhat extreme natural conditions. Snails either freshly caught or kept overnight in a jar partly filled with sea-water were dried with blotting-paper and distributed among a number of small dishes of known weight. After the dishes containing the snails had been weighed, they were put in the sun outside the laboratory at St. James, at a spot not far from the upper limit of the *Littorina* zone. The dishes were weighed at intervals and the water lost was determined, and was expressed as a percentage of the wet weight at the beginning of the experiment. Relative humidity of the air during the experiment was measured by means of a self-recording hygrometer placed among the dishes; this varied from 42 per cent. to 90 per cent. *L. knysnaënsis* was omitted from this experiment, since laboratory experience had shown that even at an accelerated rate of desiccation the species lived for several days.†

The results of this experiment are summarised in Table II.

From the results of the desiccation experiments described on p. 258 and 260, the following values can be obtained, showing the approximate percentage of water-loss which is harmful:—

<i>O. sinensis</i>	3-9
<i>C. cincta</i>	10-13
<i>O. tigrina</i>	7-11, 12
<i>T. dubia</i>	15-24
<i>O. variegata</i>	12-21

* It may be noted that on the shore specimens of *L. knysnaënsis* in a resting condition in dry places (Pl. LII, fig. 1) often seal the mouth of the shell on to the rock by a rim of hardened mucus. This habit, which is also known in European species of *Littorina*, may serve primarily to attach the snail to the rock, but it appears incidentally to reduce still further the loss of water by the snail.

† The results of an experiment carried out by N. A. H. Bokenham (unpublished), which was started in the summer months, with individuals of *L. knysnaënsis* kept in open dishes at room temperature, and in which the snails were transferred to sea-water for a short time once a week, showed that some individuals survived for as long as 22 weeks. Experiments by the present author, in which the snails were constantly kept

TABLE II.

Desiccation Experiment on the Shore.

Species.	Number of hours of desiccation.	Water-loss as percentages of initial wet weight.	Number of observations.
<i>O. sinensis</i>	1.5	1.9-3.7, average 3	8
	2.5	3.7-5.4 " 5	8
	4	4.8-7.0 " 6	8
	5	5.4-7.8 " 7	5
<i>C. cincta</i>	2	6.9- 8.3 " 8	8
	4	9.2-11.3 " 10	8
	5	11.9 " 12	1
	5.5	10.4 " 10	1
	6	11.1-13.1 " 12	5
<i>O. tigrina</i>	1.5	3.3- 5.9 " 5	9
	2.5	4.7- 8.8 " 7	9
	4	7.7-12.4 " 10	9
	5	8.7-13.5 " 10	8
	6	9.4-11.7 " 11	4
<i>T. dubia</i>	1.5	3.4- 4.1 " 4	8
	2.5	4.9- 5.7 " 5	8
	4	6.6- 7.9 " 7	8
	6	8.4-10.3 " 10	8
	7	9.1-10.2 " 10	4
<i>O. variegata</i>	2	5.8- 8.4 " 7	6
	3.5	9.4 " 9	1
	4	8.4-12.6 " 10	6
	5	10.5-14.3 " 12	4
	6	10.4-12.9 " 12	3

The number of snails in each dish was: *O. sinensis* 7, *C. cincta* 10, *O. tigrina* 8, *T. dubia* 10, 12, 14, 16, and 20, *O. variegata* 10.

The dates on which the observations were carried out were: *O. sinensis* 16/1/39, *C. cincta* 30/12/38, *O. tigrina* 16/1/39, 18/1/39, *T. dubia* 31/1/39, *O. variegata* 29/12/38.

Taking the time which elapses between one high water and the next as approximately 12.5 hours, the times of exposure which are harmful for the mature individuals of the various species under more or less extreme under dry conditions in the laboratory, showed that some survived for 7 weeks (temp. ± 17 to $\pm 31^{\circ}$ C.), while others died within the second week (temp. ± 18 to $\pm 31^{\circ}$ C.). According to Bavay (1920) *L. muricata* can survive desiccation for more than a year.

conditions can be expressed as percentages of the tidal period. Bokenham and Neugebauer have worked out the amount of exposure to which the various levels at which the several snails occur are actually subjected. They expressed the exposure as percentage exposure over one year. The values obtained by the present author and those obtained by Bokenham and Neugebauer have been combined in Table III.

TABLE III.

Exposure-data for the Several Levels at which the Different Snails Occur, Compared with the Amount of Exposure which is harmful for these Species.

Species.	Percentage of exposure of levels at which the species occurs (percentage of a period of one year, Bokenham and Neugebauer).	Approximate exposure at which death occurs (percentage of one tidal period).
<i>O. sinensis</i> . .	0-45, without distinct maximum at any given point.	12-> 60
<i>C. cincta</i> . .	0-90, with a maximum at about 35.	32-> 60
<i>O. tigrina</i> . .	10-95, without a distinct maximum.	20-48
<i>O. variegata</i> . .	From less than 5 to 100, with a maximum at about 35.	48-> 100
<i>T. dubia</i> . .	From less than 5 to 100, with a maximum at about 35.	> 56-> 100
<i>L. knysnaënsis</i> .	10-100, with a maximum at about 95-100.	> 100

Before considering the data combined in the above table it should be stressed that the figures obtained by Bokenham and Neugebauer only give the amount of exposure of the *level* at which the several snail species occurred in the traverses studied. In the case of the moisture-loving snails (*O. tigrina*, *O. sinensis* (Pl. LIII, fig. 2), and *C. cincta*), primarily frequenting pools and crevices, these values do not correspond with the amount of exposure to which the snails themselves are subjected.*

The agreement between the two columns of Table III, with respect both to sequence and to the variation within each species, though not particularly close, is nevertheless closer than might be expected from

* Stephenson points out this fact for *O. tigrina* in discussing the results obtained by Bokenham and Neugebauer (Bokenham, Neugebauer and Stephenson, 1938, p. 130). *C. cincta* and *O. sinensis*, however, should be subjected to a similar reservation. These two species inhabit a lower level than *O. tigrina* and therefore the difference will be less than in the case of the latter, but nevertheless will exist.

data of so different a nature, when the considerations just mentioned are borne in mind. Only in the case of *O. tigrina* is there any fundamental disagreement, and this might be expected after what has already been said. In the case of *T. dubia* it will be seen that Bokenham and Neugebauer found that the bulk of individuals occurred at a level subject to about 35 per cent. exposure. This exposure-time seems to be somewhat low when compared with the data in the next column of Table III. This suggests the action of another factor, which in this case seems to be of greater importance than desiccation in the control of the distribution.*

To obtain an idea of the differences in humidity of the air in the different zones, records were made with a self-recording hygrometer on the 6th of February 1939. This was a cloudless and very warm day, with a moderate S.E. wind. The water was exceptionally low. The humidity readings were made by transferring the hygrometer from one zone to another in the course of a rather short time (altogether about twenty minutes or less). The readings gave the following results: Upper limit of Littorina zone, 74 per cent. to 76 per cent.; upper limit Balanoid zone, 80 per cent.; lower limit Balanoid zone, about 83 per cent.; *Patella cochlear* zone, about 76 per cent. As can be seen, there is relatively little difference between these readings, and this seems to show that, as far as unprotected spots are concerned, local zonal differences in humidity of the air are swamped by the influence of even a moderate S.E. wind, the prevailing wind during the summer months.

Conclusions.

1. The results of the above experiments show that in five of the six species (*O. sinensis*, *C. cincta*, *O. variegata*, *T. dubia* and *L. knysnaënsis*) there is a definite correlation between the zonal distribution and the resistance to desiccation. This connection is most marked in the case of *L. knysnaënsis*, which inhabits the highest intertidal levels and which appears to be very efficiently protected against desiccation.

2. Except in *L. knysnaënsis* there is very little correlation between the vertical distribution and the rate at which water is lost.

3. In four of the six species (*O. sinensis*, *C. cincta*, *O. variegata* and *L. knysnaënsis*) there is a rough parallel between the amount of exposure which the mature snails were found to be able to endure in the experiment carried out under normal conditions, and the relative amounts of exposure

* This factor is very likely the food-supply of this species. These snails feed chiefly on barnacles and small specimens of the limpet *Patella granularis* Linn., which are very abundant in the lower Balanoid zone (Pls. LII, fig. 3 and LIII, fig. 1). It therefore seems very likely that the majority of individuals of *T. dubia* are kept at a lower level than that to which desiccation would permit them to go, by the intertidal position of their chief food-supply.

to which they are subjected in their natural habitats. This does not apply to *O. tigrina* and to the bulk of individuals of *T. dubia*, for reasons which are discussed.

4. It may be concluded that *L. knysnaënsis* is able to inhabit high levels because of its efficient resistance to desiccation; that *O. variegata* and *T. dubia* are both able to extend to fairly high levels in accordance with a fairly high resistance to desiccation, although the bulk of the population of the latter tends to occur lower down than its desiccation-resistance would permit, because its main food-supply is rather low down; and that *O. sinensis*, *O. tigrina* and *C. cincta* are debarred from the higher levels because their resistance to desiccation is low, except in so far as they can colonise pools at such higher levels.

TEMPERATURE.

Introduction.—Several authors working on marine intertidal molluscs have demonstrated different lethal temperatures for species inhabiting different levels on the shore (Gowenlock and Hayes, 1926; Gowenlock, 1926; Henderson, 1929). Gowenlock and Hayes found differences even between the temperatures lethal to individuals of the *same* species collected from different levels. The above-mentioned authors determined the temperatures lethal to snails when submerged. Although none of them seem to have taken temperature readings in the different habitats of the snails dealt with, it is very likely that the temperature range differed in the several habitats during low water, and that these differences would show a correlation with the differences in the lethal temperatures.

In the case of the six gastropods which form the subject of this paper, the lethal temperature for each species when submerged, as well as the resistance to prolonged high temperatures, was determined. Moreover, a number of temperature readings were carried out in the habitats of the several species in order to see whether differences occurred.

The Lethal Temperature for each Species when Submerged.—The snails brought in from the shore were kept for one or two days (never more than two days) under laboratory conditions, before being used for the experiments. For each experiment ten active individuals were put into a fairly large beaker containing sea-water, and this was kept afloat in a larger beaker partly filled with tap-water, which was heated. In this way it was possible gradually to increase the temperature of the sea-water containing the snails. This was done fairly rapidly until a temperature of 19 to 22° C. was reached. Subsequently the rate of increase in temperature was slowed down to an average of about 1° C. per five minutes. This was considered to be slow enough to make the difference between the body-temperature of the snails and the temperature of the surrounding water,

if existing, so small that it could be neglected. Notes were made on the behaviour of the snails during the heating. After the heating the water was allowed to cool down. The sea-water was stirred vigorously at intervals during the period of heating and cooling. After each experiment the number of snails which showed signs of life when touched was recorded. It may be stressed here that in this way the temperature lethal to *submerged* snails only is determined. The lethal temperature for snails under dry conditions may be somewhat different, but is very hard to determine, because (a) a gradual and regular increase in temperature is difficult to obtain, and (b) an increase in temperature leads to accelerated desiccation. The results of the lethal-temperature determinations are given in Table IV.

TABLE IV.

Lethal-temperature Determinations.

Species.	Temperature at which activity stopped.	Lowest temperature at which death occurred.	Temperature at which all snails were dead.
<i>L. knysnaënsis</i>	35.7-40.7° C.	47.4° C. (90-100% alive).	48.6° C.
<i>O. variegata</i>	37.2-> 41.5° C.	41.5° C. (80% alive).	42.1° C.
<i>T. dubia</i>	36.0-39.4° C.	41.2° C. (80-90% alive).	41.7° C.
<i>O. tigrina</i>	36.8-> 38.3° C.	38.9° C. (90-100% alive).	40.5° C.
<i>C. cincta</i>	36.3-38.0° C.	38.9° C. (67% alive).	± 39.5° C.
<i>O. sinensis</i>	35.4-> 39.0° C.	38.0° C. (80% alive).	39.6° C.

The results given in the last column of this table are graphically represented in fig. 5. They are in accordance with what would be expected if the distribution of the snails be taken into consideration. *L. knysnaënsis* reaches such high levels that some of the individuals are washed only by the waves during high tide when the wave-action is considerable. The lethal temperature for submerged individuals of this species appears to be very high, namely, about 48° C. Next comes *O. variegata* with a lethal temperature of about 42° C., closely followed by *T. dubia* with a lethal temperature slightly lower than 42° C. The zones of these two species overlap a great deal (see fig. 1), and only a slight difference, if any, is to be expected. Next in order comes *O. tigrina*, which has a lethal temperature of about 40° C., followed by *C. cincta* and *O. sinensis*, both with a lethal temperature of approximately 39° C.

From the distribution of the two latter species as given in fig. 1, and from the results of the temperature readings in the different habitats (p. 274), a greater difference in lethal temperature between these species

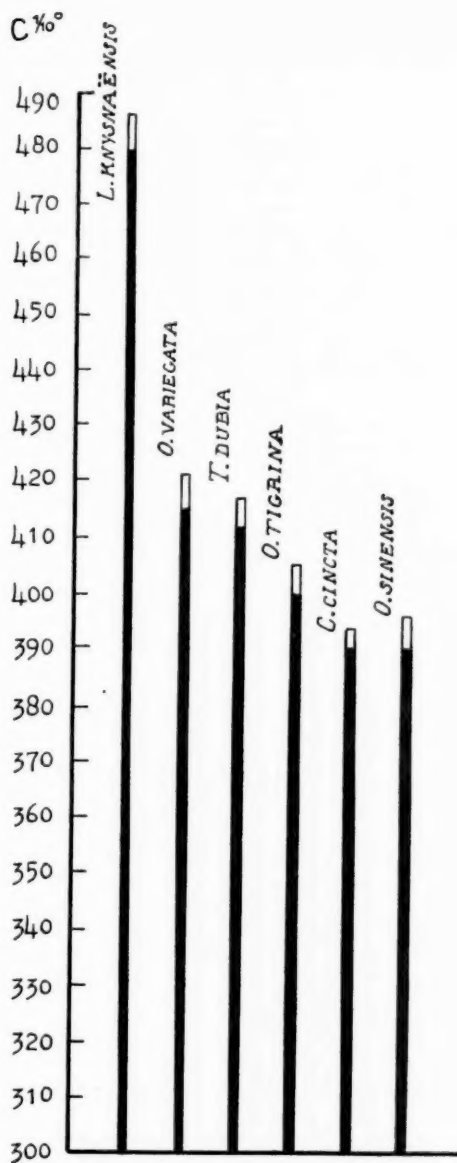


FIG. 5.—The lethal temperatures for the several species. The exact lethal temperatures lie somewhere in the white parts of the diagram.

was possibly to be expected. It must, however, be kept in mind that fig. 1 is based on a few traverses only, and probably exaggerates the difference in distribution between these two species. The majority of individuals of *C. cincta* at St. James are found in cracks inhabited by dense populations of the sea-anemone *Bunodactis reynaudi* (M. Edw.), or in crevices in the dense beds of *Mytilus perna* (Linn.), both of which are at only a slightly higher level than the zone of *O. sinensis* and therefore remain, even at low water, in fairly close contact with the regulating influence of the sea. Only a few individuals of *C. cincta* inhabit pools at higher levels.

When the temperatures at which signs of activity ceased are compared for the several species, it will be clear that no definite sequence can be found.

The Resistance to Prolonged High Temperatures.—In order to test the resistance of the several species to temperatures somewhat below the lethal temperature, the following experiment was carried out.

A number of individuals of each species, submerged in sea-water, were heated fairly rapidly until a temperature of about 20° C. was reached. From then onward the rate of increase of temperature was slowed down to an average of about 2° C. per five minutes. After the required temperature had been reached, it was kept as constant as possible for the duration of the experiment. In most cases it was possible to keep the temperature constant to within a degree. At intervals a number of snails were removed, the water in the dish containing them was allowed to cool down, and the number of individuals which were still alive was then recorded. The technique of heating was the same as in the experiments described above. Aeration was effected by means of a stream of bubbles. As a change in salinity could be expected during the several hours of heating, the salinity of the water at the beginning and at the end of the experiment was determined.

The results are given in Table V.

This table shows that the resistance of the several species to prolonged high temperatures, while submerged, is considerable. When the species are compared it will be seen that they show a sequence which is the same as the one found for the lethal temperatures.

Temperature Readings on the Shore.—Temperature readings in the different habitats were taken at low water on five different days. These days were so chosen that they represented different meteorological conditions. As lethal temperatures and resistance to high temperatures had been determined for only submerged individuals, only *water temperatures* in the different habitats came into consideration. It was, however, difficult to obtain water-temperature readings for the species *O. variegata* (Pl. LII,

TABLE V.

*The Resistance of the Several Species to Prolonged High Temperatures.**

Species.	Temperature in °C.	Time of exposure in hours.			
		½.	1.	2.	3.
<i>L. knysnaënsis</i>	37-38	5r	5r	5r	2 to 3r, rest a
	39-40	6r	..	5r	5r
	43-44	3r, 2a	5a	3a, 2d	5a
<i>O. variegata</i>	37-38	5r	5r	4r, 1a	5a
	39-40	4r, 1a	..	5d	5d
<i>T. dubia</i>	35-36	5r	5r	5r	5r
	37-38	5a	..	1a, 4d	..
	39-40	5d	5d	5d	5d
<i>O. tigrina</i>	35-37	5r	5r	4a	4a, 1d
	36-37	..	5a	4a, 1d	5d
	37-38	1r, 2a	5a	5d	5d
<i>C. cincla</i>	35-36	5r	5a	5a	5d
	37-38	5d	5d	5d	..
<i>O. sinensis</i>	35-37	4r, 1a	5a	5a	5d
	36-37	4a, 1d	..	5d	5d
	37-38	2a, 4d	5d

fig. 2) and *T. dubia* (Pl. LII, fig. 3), which are seldom found in pools,† and this is the reason for the rather small number of temperature readings for these two species. *L. knysnaënsis*, although on the whole a species which prefers exposed positions, is also very often found in the highest intertidal pools, and water-temperature readings could easily be obtained for this species.

The results of the temperature readings are recorded in Table VI.

* r means that the snails recovered fully after having been transferred gradually to ordinary sea-water; a means that the snails were alive although they did not recover fully; d means that no sign of life could be detected. The greatest recorded difference between the salinity of the water at the beginning of an experiment and at the end was 2.5 Cl/L.

† This was also observed by Bokenham and Neugebauer and is clearly demonstrated in their fig. 7.

These readings show that the range of water temperatures of the pools in the habitats of the different snails differ markedly, especially on warm days when low water occurs at about noon. It is also clear that on the whole these temperature ranges correspond with the zonation of the six species on the shore.

This is especially well shown by the readings taken on 1/10/38. If the differences between the extreme water-temperature readings for each zone on that day are calculated, the following figures are revealed:—

<i>L. knysnaënsis</i>	9.0° C.
<i>T. dubia</i>	7.4° C.
<i>O. variegata</i>	6.9° C.
<i>O. tigrina</i>	4.2° C.
<i>C. cincta</i>	3.5° C.
<i>O. sinensis</i>	0.2° C.

The number of readings for *L. knysnaënsis* on that date was much greater than in the case of the other species. This is due to the fact that in this species temperature readings were particularly easy to obtain (see p. 273) and that a great temperature range was expected. In the above-mentioned figures an irregularity appears in the cases of *T. dubia* and *O. variegata*, if we consider their vertical distribution as shown by fig. 1. According to this figure *O. variegata* reaches a slightly higher level than *T. dubia*. The difference between the two temperature ranges, however, is only 0.5° C., while, as has been pointed out before, the habitats of these two species overlap to a great extent.

If the temperature ranges calculated from the combined readings of all the five days (third main column of Table VI) are compared, a correlation between the sequence of these ranges and the zonal distribution is clear for four of the six species (*L. knysnaënsis*, *O. tigrina*, *C. cincta* and *O. sinensis*), *T. dubia* and *O. variegata* showing a disagreement. As has been pointed out, the number of water-temperature readings for the last two species is small, as they are inclined to avoid pools during the low-water period; this may be the explanation of the irregularity.

From the above it may be concluded that, on the whole, there is a correlation between the water temperature of intertidal pools in the several habitats, the temperatures lethal to mature individuals of the different snails when submerged, and the ability to resist prolonged high temperatures.

This correlation is specially important in the case of the moisture-loving species (*O. sinensis*, *C. cincta* and *O. tigrina*), as water temperatures may play a part in controlling the distribution of these snails on the shore. This partly holds also for *L. knysnaënsis*, as a fair number of individuals of this species can be found feeding in the highest intertidal pools during

low water. The observations described above, however, are only of a limited value as regards *T. dubia*, *O. variegata* and many individuals of *L. knysnaënsis*, because of the preference of these species for exposed positions at low water. In these cases air temperatures are likely to be of more importance than water temperatures.

Although it is hardly possible to state whether temperature can act as a limiting factor in the distribution of a species, unless the influence of this factor on all the different stages of development and also in combination with other factors has been studied, the above-mentioned experiments give reason to believe that the influence of temperature (acting as a separate factor) is rather limited, at least in the three moisture-loving species. The factor of safety seems to be too high to make one expect a direct influence of temperature on mature individuals as a limiting factor, and it seems more likely that the above-mentioned correlation is a secondary one.* The action of temperature may, however, be of more importance in the case of the immature and larval stages. It has, for instance, been found by Vernon (1899) working with echinoid larvae, and Andrews (1925) working with *Thaumantias cellularia* Haeckel, that the lethal temperatures for the different larval stages showed differences, the lowest lethal temperature being found in the case of the youngest developmental stages. If this holds good for molluscs, temperature may act as a limiting factor in the distribution of the veliger larvae, or of slightly more advanced developmental stages of the snail, and in that way may indirectly restrict the distribution of the mature individuals of the several species under consideration. This would especially be the case if a species does not disperse very much after the veliger has settled down (Herdman, 1890; Mitsukuri, 1901). More detailed work is therefore necessary before a more positive statement can be made, and it is hoped to deal with this at a later date.

It is interesting to compare the lethal temperatures found for the six gastropods in question with the temperatures lethal to other marine molluscs. The results given in this paper, therefore, have been combined in Table VII with those of Vernon (1899), Gowenlock and Hayes (1926), Gowenlock (1926), and Henderson (1929). A comparison such as this has a limited value as the techniques used by the several authors are not exactly the same. They all, however, gave the lethal temperature for submerged individuals, and the differences will therefore be chiefly found in the rate of increase in temperature.

This table gives a good idea of the differences in lethal temperatures which exist

* Mayer (1914) showed that "the factor of safety in respect to elevation of temperature is far less in tropical than in temperate animals." It would be interesting if the above-mentioned gastropods could be compared in this respect with forms occurring in the intertidal zone of a tropical part of the African coast, but as far as the present author knows no such observations are available.

TABLE VII.

Temperatures Lethal to Various Marine Molluscs when Submerged.

Level.	Species.*	Lethal temperature (°C.).	Locality.	Author.
Sublittoral	<i>Venus mercenaria</i> (L.)	45.2	St. Andrews, N.B.	Henderson
	<i>Yoldia sapotilla</i> (Gould)	34.8	"	"
	<i>Musculus niger</i> (Gray)	34.5	"	"
	<i>Pandora trilineata</i> Say	33.5	"	"
	<i>Astarte undata</i> (Gould)	33.5	"	"
	<i>Cardium pinnulatum</i> Conrad	33.2	"	"
	<i>Crenella glandula</i> (Totten)	32.8	"	"
	<i>Saxicava rugosa</i> (L.)	32.8	"	"
	<i>Leda tenuisulcata</i> (Couthouy)	32-31	"	"
	<i>Musculus discors</i> (L.)	31.9	"	"
Lower intertidal zone †	<i>Littorina littorea</i> (L.)	44-41	"	Gowenlock and Hayes
	<i>Littorina littorea</i> (L.)	46.6	Halifax	"
	<i>Macra solidissima</i> Dillwyn	37	St. Andrews, N.B.	Henderson
	<i>Modiolus modiolus</i> (L.)	36.3	"	"
	<i>Zirfaea crispata</i> (L.)	35.5	"	"
	<i>Oryzetele sinensis</i> (Gmelin)	39.6-39.0	False Bay, S.A.	Broekhuysen
	<i>Cominella cincta</i> (Röding)	39.4-39	"	"
Mid-tidal zone †	<i>Littorina saxatilis</i> (Oliv.)	43.3-42.3	St. Andrews, N.B.	Gowenlock and Hayes
	<i>Littorina palliata</i> (Say)	42.5-41.8	"	"
	<i>Oryzetele variegata</i> (Anton)	42.1-41.5	False Bay, S.A.	Broekhuysen
	<i>Thais dubia</i> (Krauss)	41.7-41.2	"	"
	<i>Oryzetele tigrina</i> (Dillwyn)	40.5-40.0	"	"
Upper intertidal zone †	<i>Littorina knysnaensis</i> Philippi	48.6-47.9	"	"
	<i>Macoma fusca</i> (Say)	42.3	St. Andrews, N.B.	Henderson
	<i>Mytilus edulis</i> (L.)	40.8	"	"
	<i>Mya arenaria</i> (L.)	40.6	"	"
Level not stated	<i>Ostrea virginica</i> Gmelin ‡	48.5	"	"
	<i>Pterotrachea coronata</i> Forskål	42.3	Naples	Vernon
	<i>Tethys leporina</i> L.	40.5	"	"
	<i>Octopus vulgaris</i> Lamarck	36.0	"	"
	<i>Cymbulia peronii</i> Blainville	35.7	"	"
	<i>Thais lapillus</i> (L.)	35.5-35	St. Andrews, N.B.	Gowenlock
	<i>Ilyanassa obsoleta</i> (Say)	± 35	"	"
	<i>Buccinum</i>	29	"	"
	<i>Doris</i>	29	"	"
	<i>Acmea</i>	29	"	"

* I am indebted to Mr. J. R. le B. Tomlin for the correct names.

† In these cases Gowenlock, Hayes, and Henderson used the term "littoral," which apparently had the same meaning as intertidal. As different authors use the term littoral in different senses it was thought to be safer to use the term intertidal.

‡ This is a warm-water species, which explains its high lethal temperature.

among molluscs. It also shows that, generally speaking, the lowest lethal temperatures are found in snails inhabiting the lowest levels, while lethal temperatures increase with increasing height above low-water level. It is evident, however, that there is much local variation.

It may be stressed here that *L. knysnaënsis* has a lethal temperature (while submerged) which is almost as high as that of the tropical Lamellibranch *Ostrea virginica*.

Conclusions.

1. There exists a correlation between the temperature ranges of the intertidal pools in the several habitats, the temperatures lethal to mature individuals of the six species studied (when submerged), and the ability of these snails to resist prolonged high temperatures.

2. Various considerations, however, lead to the conclusion that the direct influence of temperature as a limiting factor in the vertical distribution of the mature snails is probably rather a limited one, at least in the case of three of the six species which form the subject of this paper.

3. In marine molluscs in general the lethal temperature seems to increase with increasing height above low-water level, while warm-water forms on the whole show a higher lethal temperature than forms occurring in colder water.

SALINITY.

Introduction.—The influence of salinity on the distribution of marine animals has been investigated rather thoroughly by various authors, and it is a well-known fact that many marine animals have a salinity optimum at which they thrive. Most of the work in this connection has been done on sublittoral and pelagic forms, but a considerable amount has also been done on intertidal species (Allee, 1923; Klugh, 1924; Gowenlock and Hayes, 1926; Pearse, 1928; Worley, 1930; Rice, 1930, etc.). Salinity conditions in the intertidal zone during low water are seldom constant, and may be expected to vary a great deal as a result of evaporation on sunny and windy days, and of dilution on rainy days.* It therefore seems likely that in the case of intertidal forms it is rather the range of salinity which a species can withstand than the existence of a particular more or less constant salinity which affects the distribution, while in sublittoral and pelagic forms it has been found that the latter factor seems to be the more essential. The range of salinity at varying levels of the intertidal zone will show differences. Species inhabiting different levels will therefore probably show divergences in the amount of variation in salinity which they can stand.

* When heavy rain falls a layer of fresh water is formed on the surface of intertidal pools, which during calm weather mixes slowly by diffusion, but on windy days mixes almost at once (see Table X, and Nicol, 1935, p. 233).

The resistance to differences in salinity was studied for mature individuals of each of the six gastropods under consideration. Two types of determinations were made: (a) of the salinities at which crawling activities ceased, and (b) of the length of time during which the different species could endure submersion in solutions of different salinities. Moreover, a number of salinity determinations were carried out in the natural habitats of the snails, at low water, under more or less extreme meteorological conditions, in order to obtain an impression of the actual changes in salinity which prevail there.

Determinations of the Salinity at which the several Species cease Crawling.—

The salinity at which the crawling of a particular snail ceases is of importance since, so long as this salinity has not yet been reached, there is still a chance for the snail to escape the detrimental influence of any change (sudden or gradual) which, if acting for some time, might prove to be fatal.* It would be expected that species occurring at different levels in the intertidal zone might show differences in the salinities which would cause their crawling activities to cease. In order to determine whether the six species which form the subject of this paper showed any such adaptations, the following experiment was carried out.

Ten freshly caught individuals of a species were put into a large petri-dish, partly filled with ordinary sea-water ($Cl = \pm 19.39$ per KG). After a short time the salinity was increased or decreased by gradually adding either concentrated sea-water or distilled water. This was continued until all ten snails had ceased crawling. The dish was then left for some time, and if none of the snails showed any crawling movement the salinity was determined by means of titration.† If any of the snails regained activity, the decrease or increase of the salinity was continued until all activity ceased permanently. Both the distilled water and the concentrated sea-water were kept for some time over shell fragments in order to keep the pH constant, and at the end of each experiment the pH was checked by means of B.D.H. Universal Indicator. The concentrated sea-water was obtained by evaporating ordinary sea-water for some time at a temperature not exceeding 65° C.

The results of this experiment are given in Table VIII, and are graphically expressed in fig. 6.

These data reveal the following facts. *L. knysnaënsis*, a species

* In the experiment described below it was noticed that an increase in crawling took place when the salinity was changed.

† In several cases the salinity was so high that the ordinary method of expressing the Cl-content in Cl/KG (Knudsen, 1901) presented difficulties. In these cases the Cl-content is given as Cl/L. In the other cases the Cl-content is given as Cl/KG as well as Cl/L.

TABLE VIII.

Determinations of the Salinity at which the several Species cease their Crawling Activities.

Species.	Salinity at which crawling ceased.				Temperature during the experiment.
	A. With lowered salinity.		B. With increased salinity.		
	Cl/KG.	Cl/L.	Cl/KG.	Cl/L.	
<i>L. knysnaënsis</i>	6.40	6.46	..	38.69 *	19-23° C.
	6.89	6.97	..	40.06 *	
	7.42	7.51	..	40.66	
<i>O. tigrina</i> †	9.58	9.71	..	33.57	22-23° C.
	9.75	9.89	..	33.88	
	10.63	10.79	..	35.51	
<i>O. variegata</i>	11.18	11.36	..	33.84 ‡	21-23° C.
	11.27	11.45	..	34.18	
	11.73	11.93	..	34.79	
<i>T. dubia</i>	10.82	10.99	..	32.14	18.5-20° C.
	11.16	11.34	..	32.32	
	11.84	12.04	..	32.68	
<i>C. cincta</i>	11.36	11.55	..	29.67	19-22° C.
	11.69	11.89	..	29.98	
	11.87	12.07	..	31.60	
<i>O. sinensis</i>	12.49	12.72 §	..	27.50	18.5-23° C.
	12.67	12.9	..	30.75	
	13.26	13.52 §	..	31.06	

* Four days after the end of the experiment the salinity in these dishes was Cl/L=45.49. After the salinity had been decreased three of the ten snails showed signs of life while the rest climbed the sides of the dish, and apparently recovered fully.

† Twenty-four hours after the experiment one of the dishes contained water of Cl/L=35.38. All ten snails were still alive.

‡ Two days after the experiment the salinity of the water had become Cl/L=34.81. After the salinity had been decreased five of the ten snails recovered fully.

§ In this case the pH was not checked.

|| Twenty-four hours after the experiment the salinity had increased to Cl/L=31.98. All ten snails appeared to be still alive.

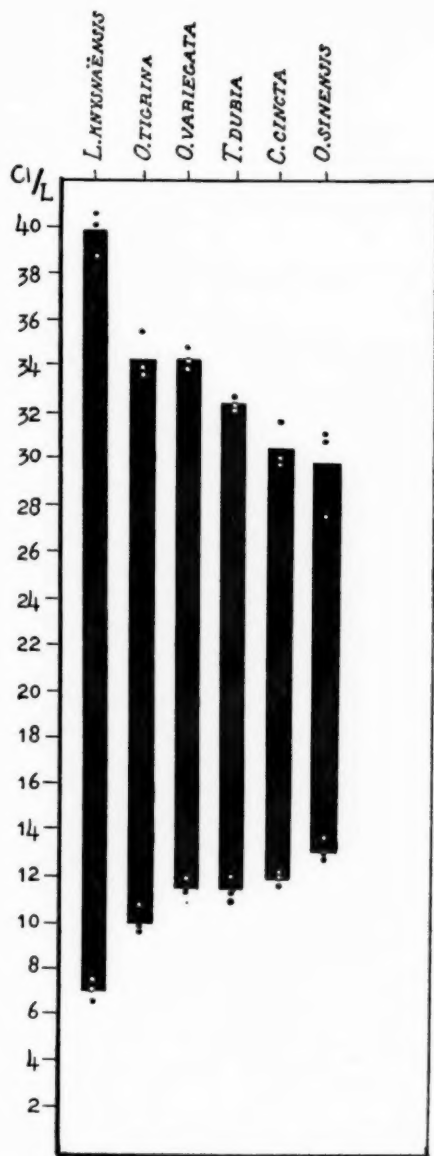


FIG. 6.—The salinities in Cl/L at which crawling is possible for the several species.

inhabiting the higher parts of the intertidal zone, can withstand a remarkable amount of variation in salinity, namely, $Cl = \pm 7$ to $\pm 39.8/L$, before crawling activity ceases. During low water the individuals of this species are found in the highest intertidal pools as well as in a dry condition attached to the rock-surface outside pools. Those in the pools are exposed to great variations of salinity, as some of the smaller pools may lose all their water by evaporation before the waves of the returning tide reach them. On rainy days the water of these pools is greatly diluted.

After *L. knysnaënsis* comes *O. tigrina* with a salinity range of $Cl = \pm 10.1$ to $\pm 34.3/L$, followed by *O. variegata* with a $Cl = \pm 11.6$ to $\pm 34.3/L$, *T. dubia* with $Cl = \pm 11.5$ to $\pm 32.4/L$, *C. cincta* with $Cl = \pm 11.8$ to $\pm 30.4/L$, and *O. sinensis* with $Cl = \pm 13.0$ to $\pm 29.8/L$. If figs. 1 and 6 be compared, it becomes clear that all species except one occur in the same order in the two figures. *O. tigrina*, which in fig. 6 comes after *L. knysnaënsis* and in fig. 1 after *T. dubia*, forms an exception. The question arises as to the reason why *O. tigrina*, although in general inhabiting a lower level than *O. variegata*, appears to be better adapted to variations in salinity than the latter. The explanation may be as follows. Although *O. tigrina* occurs rather high up in the intertidal zone, this species most often inhabits pools. Being therefore in close contact with the water of the pools, it is subjected to considerable variations in salinity, partly due to evaporation but chiefly due to dilution of the water by rain. The bulk of the individuals of *O. variegata* on the contrary, many of which occur at a higher level, prefer exposed and bare rock-surfaces (Pl. LII, fig. 2). Only a minority are found in the higher pools. The individuals of this species therefore must be able to withstand a certain degree of increase in salinity, in the sense that (a) some of the water retained within the shell is lost by desiccation during the exposure period, and (b) some of them do inhabit pools. On rainy days, however, most of the rain-water runs down the rock-surface without affecting the snails on the bare rock very much, since they are protected by their shells which adhere closely to the substratum. The few occurring in the higher pools will be affected by the dilution of the water, but they form only a minority. Therefore it seems understandable that in general *O. tigrina* should show a better adaptation to variations in salinity than *O. variegata*, and that the difference should be found chiefly in ability to withstand lower salinities.

Resistance of the Different Species to Extreme Salinity Conditions.—The above experiment made it probable that the different snail species would also show a sequence in the length of time for which they could resist unfavourable salinity conditions. To obtain comparative data in this connection it was necessary to keep the snails submerged for some time. As they are all intertidal species, and as at least several of them are exposed

to the air for a considerable time daily, it was first necessary to determine the time during which each species could be kept submerged without ill-effects. The difficulty arose of how to keep the snails under water and yet to aerate the water sufficiently without causing any accumulation of air. This difficulty was solved by the following arrangement. Two large jars, each containing sea-water, were placed one above the other, being connected with each other by rubber and glass tubing. The water of the lower could flow into two glass tanks, also filled with sea-water, by means of rubber and glass tubes, which eventually led into four pipettes (two in each glass tank) the tips of which had been turned upwards. Finger-bowls were put over these pipettes. Each tank therefore contained two inverted finger-bowls which were submerged (care being taken that they did not contain air), and under which the water was continually replaced by fresh sea-water from the two jars. When the water in the glass tanks had reached a certain level an overflow began to work, and the water was collected in two large vessels standing on the ground. When the jars were nearly empty they were filled again with the water collected in the lowest vessels. In this way the water was circulated periodically. Supplementary aeration could be given by means of an adjustment on the lower of the two jars. The water in the jars as well as in the tanks containing the finger-bowls was kept above shell-fragments in order to keep the pH constant. The salinity of the water was determined at intervals in order to avoid too great a variation due to evaporation. The snails which had to be tested were put under the finger-bowls, while an equal number were kept in the lowest vessels as a control. These latter were subjected to an artificial tide, due to the gradual filling up of the tanks and their subsequent emptying. These snails were free to crawl out of the water.

The results of this experiment demonstrated that all the species could stand submersion for over a month, the experiment being stopped after this period. Although no food was given, all the individuals appeared to be quite healthy at the end of the experiment, and no difference from the control snails was noticeable. The number of individuals tested was two for each species except *L. knysnaënsis*, of which eight individuals were tested.

After it had been found that all the species could be kept continually submerged for at least a considerable time, if not indefinitely, it was possible to determine their degrees of resistance to extreme salinities by exposing them to such. The different solutions were made up by mixing distilled water with sea-water which had been concentrated by evaporation at a temperature not higher than 70° C. The glass vessels which contained the different solutions were put in a large thermostat, which could hold five of them at a time. The temperature had to be kept constant, as

Broekhuysen (1936), working with eggs of the crab *Carcinides (Carcinus) maenas* (L.), has pointed out the existence of a close interaction between salinity and temperature. In the salinities at which the snails retained their crawling activities they were prevented from crawling out of the water by placing them under inverted finger-bowls, which were partly lifted up from the bottom of the basin by means of shell-fragments and pieces of glass tube. Where the salinity was so extreme that crawling ceased, no finger-bowls were used. The water in each of the vessels was aerated by means of a stream of bubbles. In the case of those containing inverted finger-bowls, these latter were lifted up several times a day in order to change the water inside thoroughly. The snails were gradually transferred to the ultimate salinities in which they were to be kept by leaving them for at least half an hour in waters of graded salinity, starting with that salinity which was nearest to that of normal sea-water.

The results of this experiment are summarised in Table IX.

TABLE IX.
*Resistance to Extreme Salinities.**

Species.	Time of submersion.																			
	Two days.										Three days.									
	Salinity in Cl/L.										Salinity in Cl/L.									
	5.8-5.9.	11.0-11.1.	13.1-13.2.	16.2-16.3.	17.8-17.9.	21.9.	27.0-27.2.	33.2.	38.9.	50.0-50.3.	5.4.	10.5.	12.8-12.9.	16.2-16.3.	17.6.	21.8.	27.0-27.2.	33.2-33.4.	39.1.	50.2-50.6.
<i>L. knysnaënsis</i>	4r	4r	4r	4r	2r 2a	4r	4r	4r	4r	4r	4r	2r	2r	..	3r	
<i>O. tigrina</i>	4r	4r	4r	4r	4r	4r	4r	3r 1a	2a 2d	4d	2r	3r	4r	4r	4r	4r	2a 1a	2a 1d	..	4d
<i>T. dubia</i>	2r 1a 1d	4r	4r	4r	4r	4r	4r	4r	2a 2d	4a	2a 2d	3r	4r	4r	4r	4r	2r 1a 1d	3a 1d	3a 1d	4d
<i>O. variegata</i>	4a	4r	4r	4r	4r	4r	4r	2r 2a	4a	4d	1r 3d	4r	4r 1d	3r 1a	2r 1d	3r 1d	4d	4d	4d	4d
<i>C. cincta</i>	2r 2a	4r	4r	4r	4r	4r	4r	4a	4d	4d	3a 1d	4r	4r	4r	4r	4r	3r 1d	4d	4d	4d
<i>O. sinensis</i>	4a	4r	4r	4r	4r	4r	4a	2a 2d	4d	4d	2a 2d	1r 3d	4r	4r	4r	4r	2r 2a	4d	..	4d

* r means that the snails recovered fully after having been gradually transferred to normal sea-water; a means that the snails were alive although they did not recover fully; d means that no sign of life could be observed. The temperature in the different series of experiments varied between 15.4 and 16.6° C.

If it is borne in mind that the salinity of ordinary sea-water expressed in Cl/L is about 19.9, it will be realised that the data presented in Table IX reveal the existence of a very high resistance against extreme salinities in all six species. In the case in which the snails were kept submerged for three days, *O. variegata* showed signs of detrimental influence at salinities of 16.2-16.3 and 17.6, which are fairly close to that of ordinary sea-water. The fact that slight pollution of the water was noticeable in these cases, as a result of its having been used before, may be the explanation for this irregularity. No similar signs of pollution were noticed in the other cases.

On the whole this experiment confirms the results of experiments summarised in Table VIII. In this case also the species can be placed in a definite order according to their degree of resistance, and on the whole the sequence appears to be the same as that shown by fig. 6.

Salinity Determinations of the Water of Intertidal Pools.—In order to obtain an approximate idea of the range of variation in salinity of the tide-pools in the habitats of the several species of snails, water-samples were collected at low water, at St. James, on four different days, two sunny and two rainy. Usually the highest pools in the different habitats were chosen, with a view to obtaining the extreme salinities experienced by each species. Water-samples were taken by means of a pipette, the end of which was kept near the snails while the water was sucked up.* The salinity was afterwards determined by titration. In the case of very high salinities these were expressed in Cl/L, in the other cases they were given as Cl/L as well as in the form of Cl/KG. The results of the salinity determinations are given in Table X.

The results given in Table X show that:

- (a) Pools at different levels exhibit differences in salinity, and these differences are sometimes very marked.
- (b) On the whole, pools at higher levels have a wider range of salinities than those lower down.

This table also emphasises the fact which has been mentioned on p. 275, that *O. variegata* and even more *T. dubia* are inclined to avoid pools during the period of low water, as only very few salinity determinations of the water of pools inhabited by individuals of these two species could be obtained.

* This was done because the salinity of the surface water and of the bottom water was sometimes different (Table X).

TABLE X.

Salinity Determinations of the Water in Pools on the Shore,
during Low Water.

Date.	Habitat of	Remarks.	Cl/KG.	Cl/L.
4/2/38	<i>L. knysnaënsis</i>	A clear sunny day with a moderate S.E. wind. Low water at 11.32 a.m. Water-samples were taken from 11.15 a.m. to 4.30 p.m.	..	21.94
			..	26.86
			..	26.91
			..	26.99
			..	28.00
	<i>O. tigrina</i>		19.44	19.99
			19.44	19.99
	<i>O. variegata</i>	
	<i>T. dubia</i>	
	<i>C. cincta</i>		19.44	19.99
			19.51	20.06
			19.56	20.12
			19.58	20.14
			20.61	21.23
<i>O. sinensis</i>	19.35	19.89		
	19.36	19.90		
	19.37	19.91		
28/7/38	<i>L. knysnaënsis</i>	Heavy rain recorded for previous day and night. First foggy, afterwards sunny. W. wind. Low water at 10.13 a.m. Water-samples taken from 10.05 a.m. to 11.18 a.m.	8.88	8.99
	<i>O. tigrina</i>		13.61	13.88
	<i>O. variegata</i>	
	<i>T. dubia</i>	
	<i>C. cincta</i>	
		
		
	<i>O. sinensis</i>		19.29	19.83
			19.31	19.85
			19.32	19.86
11/8/38	<i>L. knysnaënsis</i>	Heavy showers of rain fell until the previous midnight. Low water at 9.28 a.m. Water-samples taken from 9.30 a.m. to 11.00 a.m.	1.33	1.36
			14.26	14.56

TABLE X.—continued.

Date.	Habitat of	Remarks.	Cl/KG.	Cl/L.
13/12/38	<i>O. tigrina</i>	Clear sunny day with fairly strong wind. Low water at 1.53 p.m. Water-samples were taken from 12.15 p.m. to 2.15 p.m.	18.04	18.51*
			18.16	18.64
			18.49	18.99
	<i>O. variegata</i>	
	<i>T. dubia</i>	
	<i>C. cincta</i>		11.24	11.42
			17.18	17.61
			18.78	19.29
			18.80	19.31
	<i>O. sinensis</i>		19.22	19.76
			19.29	19.83
			19.37	19.91
	<i>L. knysnaënsis</i>		19.29	19.83†
			20.88	21.51
			23.45	24.24
			22.42	23.14
	<i>O. tigrina</i>		18.60	19.10
			19.16	19.69
			16.84	17.25
			19.44	19.99
			19.81	20.38
			19.68	20.24
	<i>O. variegata</i>		19.63	20.19
			19.49	20.04‡
			19.29	19.83
			18.60	19.10
			19.76	20.33
	<i>T. dubia</i>		19.76	20.33
	<i>C. cincta</i>		19.16	19.69
			19.81	20.38
			19.56	20.10
	<i>O. sinensis</i> §		19.32	19.86

* Salinity at the surface of the pool was Cl=6.44/KG; the pool was about 2 inches deep.

† Salinity at the surface of the pool was Cl=19.17/KG.

‡ Salinity at the surface of the pool was Cl=19.17/KG.

§ This species was submerged by the sea and the salinity given is that of the sea.

The results of the three series of experiments described above have been combined in Table XI.

TABLE XI.

The Relation between Resistance to Extreme Salinities and Range of Salinities encountered under Natural Conditions.

Species.	Average salinities at which crawling ceased (Cl/L).	Salinities in which a submersion of two days had no harmful effect (Cl/L).*	Extreme salinities of the habitats (Cl/L).
<i>L. knysnaënsis</i>	7-40	6-50	1-28
<i>O. tigrina</i> .	10-34	6-27	14-20
<i>T. dubia</i> .	11-32	11-33	?
<i>O. variegata</i> .	12-34	11-27	?
<i>C. cincta</i> .	12-30	11-27	11-21
<i>O. sinensis</i> .	13-30	11-22	19

The value of this table is limited by the fact that the various sets of data were not obtained under uniform temperature conditions, since it has been proved that temperature can have a distinct influence on the resistance of certain organisms to extreme salinities (Broekhuysen, 1936). Nevertheless the data seem to show that at least in four (*L. knysnaënsis*, *O. tigrina*, *C. cincta*, and *O. sinensis*) of the six species under consideration the "facto of safety," especially towards the higher salinities, is considerable.

If the order in which the six species can be placed according to their degree of resistance to abnormal salinities is compared with the order shown by fig. 1, it will be seen that the only important difference is found in the case of *O. tigrina*, which, in ability to withstand salinity changes, comes after *L. knysnaënsis*, and in vertical distribution, between *T. dubia* and *C. cincta*. In the section dealing with desiccation, it was shown that *O. tigrina* had very little resistance to that factor (p. 269). It was therefore concluded that desiccation probably played a minor rôle in the distribution of this species. As *O. tigrina* has the highest degree of resistance to salinity variations of all the six snails except one (*L. knysnaënsis*), it is very likely that salinity plays an important part in the distribution of this species.

The change of position shown by *O. variegata* and *T. dubia* is probably due to the fact that their zones overlap a great deal and the latter is commonly kept down at a lower level by the food factor.

* The three-day submersion results are omitted on account of the inaccuracy with respect to *O. variegata*.

Conclusions.

1. The six species under consideration cease crawling at different salinities. These differences show, on the whole, a correlation with the vertical distribution of the species, *O. tigrina* being the only important exception.

2. The several species show differences in their ability to resist prolonged abnormal changes in salinity, the sequence being the same as in the case of 1.

3. Determinations of salinities under natural conditions reveal differences in salinity between pools situated at different levels, the salinities at higher levels having on the whole a wider range than those lower down.

4. In the case of *O. tigrina*, salinity seems to play an important rôle in the vertical distribution of the mature individuals. In the case of the other species this is doubtful.

SUMMARY.

A preliminary experimental study of six species of Prosobranch gastropods inhabiting the intertidal zone in False Bay has been made, the species being *Littorina knysnaënsis*, *Thais dubia*, *Oxysteles variegata*, *Oxysteles tigrina*, *Oxysteles sinensis*, and *Cominella cincta*. The sequences into which these species fall when classified according to their abilities to resist abnormal conditions are compared with the order of their zonation on the shore. The experiments were confined to adult individuals, but it is hoped in the future to extend them to the larvae, whose reactions may be different.

Desiccation.

The species exhibit a graded resistance to desiccation. *L. knysnaënsis* and *O. variegata* are able to colonise dry situations at high levels on the shore, and this distribution is correlated with high ability to withstand desiccation. Conversely, *C. cincta* and *O. sinensis* have low resistance to desiccation, and these are confined to the lower wetter parts of the shore. *T. dubia* has a high resistance to desiccation, and some individuals do occur at high levels in dry places, but the bulk of the population occurs lower down, apparently because the main food-supply occurs well below the upper limit which this species is able to colonise. *O. tigrina*, although living at fairly high levels, occurs typically in pools, and its low resistance to desiccation is therefore intelligible.

Temperature.

This has been studied only in so far as it affects submerged snails. The species show a graded series of adaptations to increased temperature, which correspond almost exactly to the gradation of their habitats on the shore; but it is probable that they rarely if ever experience water-temperatures, on the shore, which are likely to be lethal, and it is concluded that the influence of temperature as a factor controlling vertical distribution is at least of secondary importance, especially in the case of the moisture-loving species *O. tigrina*, *O. sinensis*, and *C. cincta*.

Salinity.

The species also exhibit a graded series of reactions to increase and decrease of salinity, which with one exception are in accordance with the gradation of their habitats. It is concluded that salinity is a matter of secondary importance as a factor limiting distribution, except perhaps in the case of *O. tigrina*, where it may be important.

The investigation described in this paper was originally suggested by Professor T. A. Stephenson, and is related to the general intertidal survey which is being conducted from this department. I have pleasure in thanking Professor T. A. Stephenson, Dr. H. Sandon, and Dr. W. E. Isaac for reading the manuscript and giving their criticism. I am also indebted to Dr. C. von Bonde for allowing me to use the Fisheries Laboratory at St. James, at which part of the research was carried out. Financial aid by the South African National Research Council made possible the construction of the thermostat used in the experiments dealt with on p. 283, and it is a pleasure to thank the Council for this invaluable support.

EXPLANATION OF THE PLATES.

PLATE LII.

- Fig. 1. *Littorina knysnaënsis* attached to the bare rock-surface in the highest part of the intertidal zone. Natural size.
Fig. 2. Individuals of *Oxystele variegata* in their characteristic habitat. Note their rather exposed position. Two-thirds natural size.
Fig. 3. Individuals of *Thais dubia* in their characteristic habitat. Note the more sheltered position. The two species of barnacles shown in the picture are *Octomeris angulosa* Sow and *Tetraclista serrata* Darwin. Natural size.

PLATE LIII.

- Fig. 1. Three specimens of *Thais dubia*, feeding on the barnacle *Chthamalus dentatus* KRAUSS. The limpet is *Patella granularis* Linn., which also forms a part of the food-supply of this carnivorous snail. Natural size.

Fig. 2. Two individuals of *Oxystele sinensis* in one of the lower intertidal pools (*Patella cochlear* zone). The limpets are *Patella cochlear* Born, each surrounded by its garden of *Gelidium pristoides* (Turn.) Ktz. One-third natural size.

REFERENCES.

- ALLEE, W. C., "Studies in Marine Ecology: Some Physical Factors related to the Distribution of Littoral Invertebrates," Biol. Bull., xlv, 5, 205-253, 1923.
- ANDREWS, F. B., "The Resistance of Marine Animals of Different Ages," Publ. Puget Sound Biol. Stat., iii, 361-363, 1925.
- BAKER, S. M., "On the Causes of the Zoning of Brown Seaweeds on the Seashore," New Phytol., viii, 196-202, 1909.
- BAKER, S. M., "On the Causes of the Zoning of Brown Seaweeds on the Seashore: II. The Effect of Periodic Exposure on the Expulsion of Gametes and on the Germination of the Oospore," New Phytol., ix, 54-67, 1910.
- BAYAY, A., "Notes sur les Littorines (Projet d'Études)," Bull. Soc. Zool., xlv, 249-255, 1920.
- BOKENHAM, N. A. H., NEUGEBAUER, F. L. M., STEPHENSON, T. A., "The Vertical Distribution of Certain Intertidal Marine Gastropods in False Bay, with Notes on the Development of Two of Them," Ann. Natal Mus., ix, 1, 113-137, 1938.
- BROEKHUYSEN, G. J., "On the Development, Growth, and Distribution of *Curcinides manas* (L.)," Arch. Néerl. Zool., ii, 257-399, 1936.
- CAUDRI, L. W. D., "Einfluss der Temperatur und des Salzgehalts auf die Sterblichkeit von Garnelen (*Crangon Crangon* L.)," Arch. Néerl. Zool., iii, 179-196, 1937.
- COLMAN, J., "The Nature of the Intertidal Zonation of Plants and Animals," Journ. Mar. Biol. Ass., xviii, 435-476, 1933.
- COWLES, R. P. A., "A Biological Study of the Offshore Water of Chesapeake Bay," Bull. U.S. Fish., xlv, 277-381, 1930.
- FERRONNIÈRE, G., "Études Biologique sur les Zones Supralittorales de la Loire-Inférieure," Bull. Soc. Sci. Nat., ii, 1, 1-451, 1901.
- GOWENLOCK, J. N., "Contributions to the Study of Marine Gastropods. II. The Intertidal Life of *Buccinum undatum*, a Study in Non-Adaptation," Contr. Canad. Biol. Fisher., N.S., iii, 1-8, 167-178, 1926.
- GOWENLOCK, J. N., and HAYES, F. R., "Contributions to the Study of Marine Gastropods. I. The Physical Factors, Behaviour, and Intertidal Life of *Littorina*," Contr. Canad. Biol. Fisher., N.S., iii, 1-8, 133-166, 1926.
- GRUBB, V. M., "Marine Algal Ecology and the Exposure Factor at Peveril Point, Dorset," Journ. Ecology, xxv, 392-423, 1936.
- HENDERSON, J. T., "Lethal Temperatures of Lamellibranchiata," Contr. Canad. Biol. Fisher., N.S., iv, 25-29, 397-411, 1929.
- HERDMAN, W. A., "Third Annual Report of the Liverpool Marine Biological Station on Puffin Island," Proc. and Trans. Liv. Biol. Soc., iv, 1890.
- HEWATT, W. G., "Ecological Studies on Selected Marine Intertidal Communities of Monterey Bay, California," Amer. Midl. Naturalist, xviii, 2, 161-206, 1937.
- HUNTSMAN, A. G., "The Vertical Distribution of Certain Intertidal Animals," Proc. and Trans. Roy. Soc. Canada, iii, 12, 4, 53-60, 1918.
- ISAAC, W. E., "Some Observations and Experiments on the Drought Resistance of *Pelvetia canaliculata*," Ann. Bot., xlvii, 186, 343-348, 1933.
- ISAAC, W. E., "A Preliminary Study of the Water Loss of *Laminaria digitata* during the Intertidal Exposure," Ann. Bot., xlix, 193, 109-117, 1935.

- ISAAC, W. E., "South African Coastal Waters in Relation to Ocean Currents," Geogr. Rev., xxvii, 4, 651-664, 1937.
- KLUGH, A. B., "Factors Controlling the Biota of Tide-Pools," Ecology, v, 2, 192-196, 1924.
- KNUDSEN, M., "Hydrographical Tables," 1901.
- MAYER, G. A., "Effects of Temperature on Tropical Marine Animals," Carnegie Inst. Publ., clxxxiii, Washington, 1914.
- MITSUKURI, K., "Negative Phototaxis and other Properties of Littorina as Factors in Determining its Habitat," Annot. Zool. Jap., iv, 1, 1-19, 1901.
- MOORE, H. B., "The Biology of *Balanus balanoides*. V. Distribution in the Plymouth Area," Journ. Mar. Biol. Ass., N.S., xx, 3, 701-716, 1936.
- NICOL, E. A. T., "The Ecology of a Salt-Marsh," Journ. Mar. Biol. Ass., N.S., xx, 2, 203-261, 1935.
- PEARSE, A. S., "On the Ability of Certain Marine Invertebrates to live in Diluted Sea-Water," Biol. Bull., liv, 405, 1928.
- PEARSE, A. S., "Observations on Certain Littoral and Terrestrial Animals at Tortugas, with Special Reference to Migrations from Marine to Terrestrial Habitats," Carnegie Inst. Year Book, xvii, 284, 1927-1928.
- PEARSE, A. S., "The Ecology of Certain Estuarine Crabs at Beaufort, N.C.," Journ. Elisha Mitch. Sci. Soc., xlv, 2, 230-237, 1929.
- PEARSE, A. S., "Estuarine Animals at Beaufort, North Carolina," Journ. Elisha Mitch. Sci. Soc., lii, 2, 1936.
- PRINGSHEIM, E. G., "Über die Transpiration bei Fucus," Jahrb. Wiss. Botanik, lxii, 2, 244-257, 1923.
- RICE, L., "Peculiarities in the Distribution of Barnacles in Communities and their Probable Causes," Publ. Puget Sound Biol. Stat., vii, 249-257, 1930.
- VERNON, H. M., "The Death-Temperature of Certain Marine Organisms," Journ. Physiol., xxv, 131-136, 1899.
- WORLEY, L. G., "Correlation between Salinity, Size, and Abundance of Intertidal Barnacles," Publ. Puget Sound Biol. Stat., vii, 233-240, 1930.
- ZANEVELD, J. S., "The Littoral Zonation of some Fucaceae in Relation to Desiccation," Journ. Ecology, xxv, 2, 431-468, 1937.

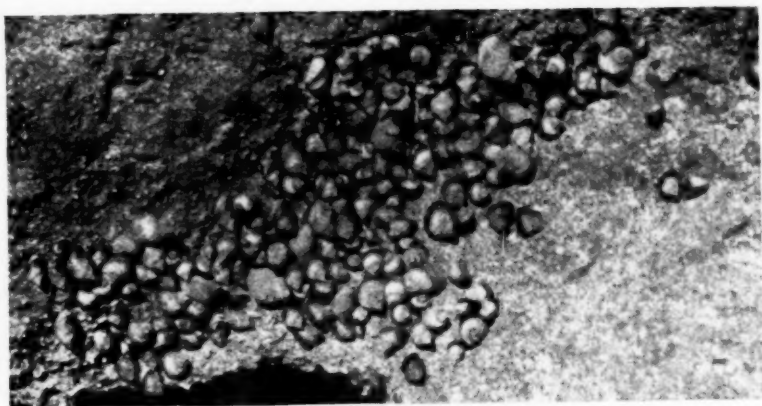


FIG. 1.

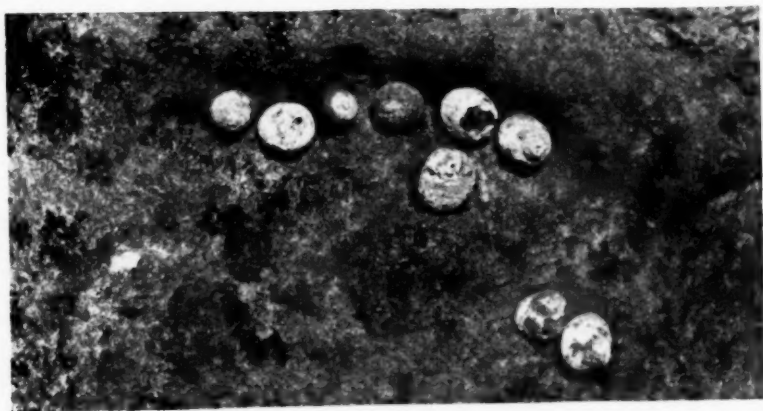
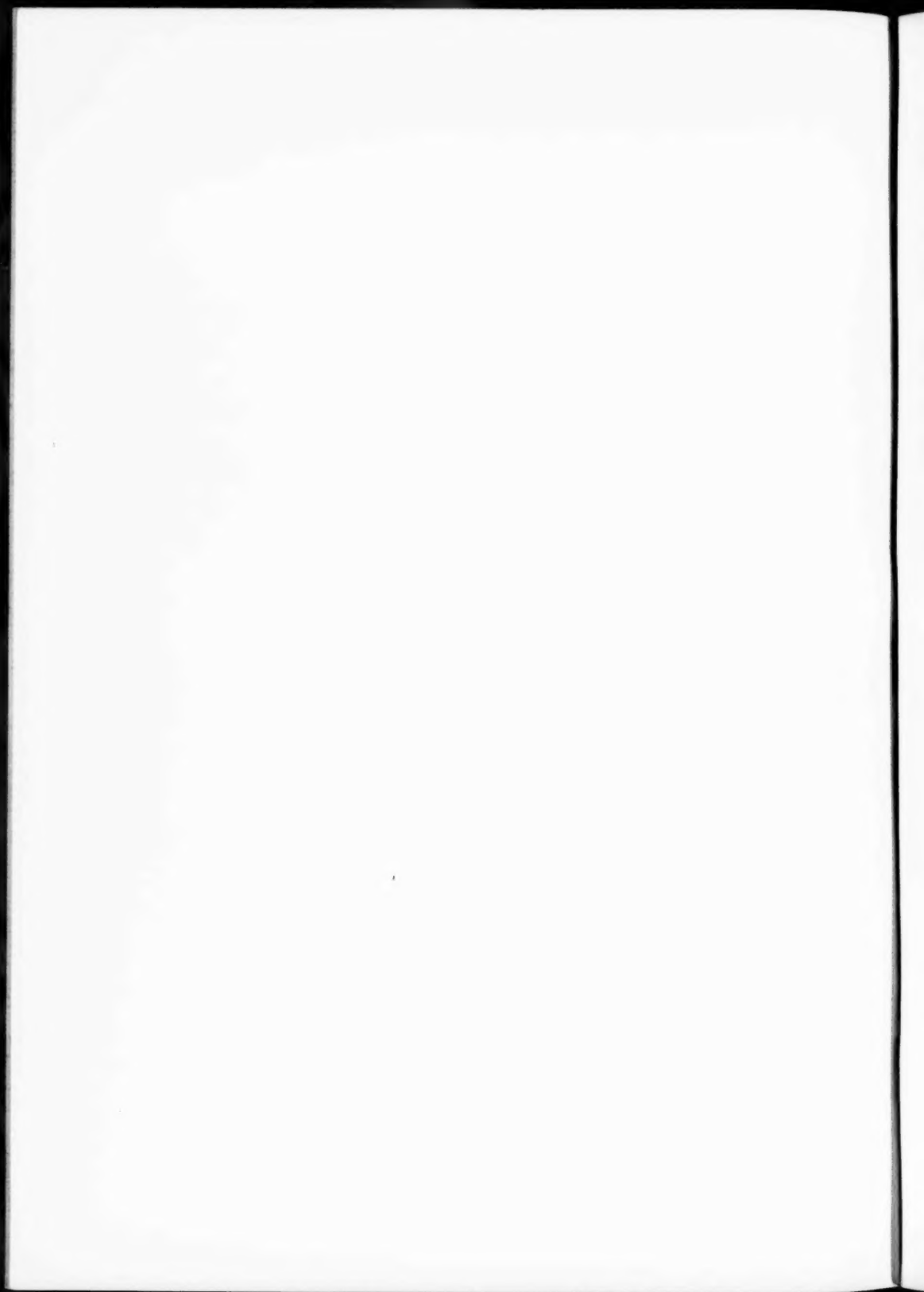


FIG. 2.



FIG. 3.



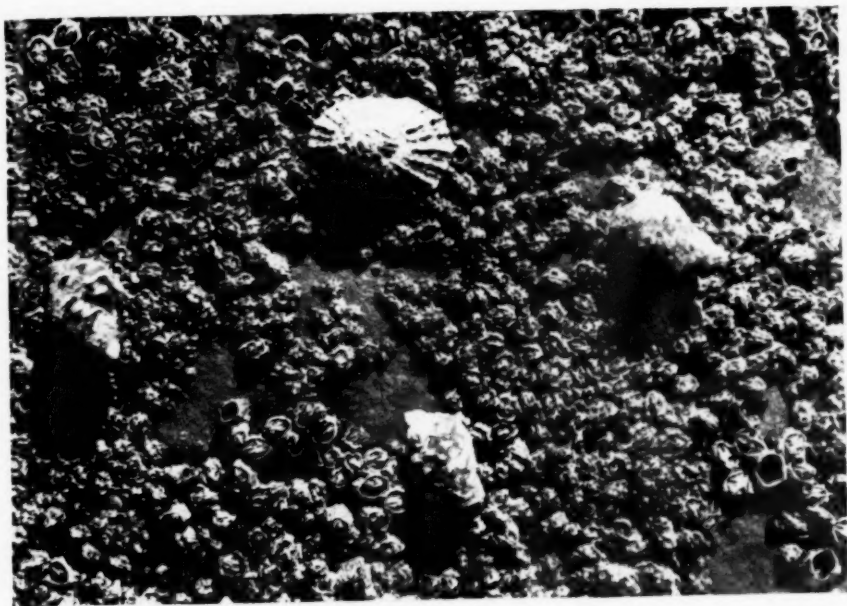
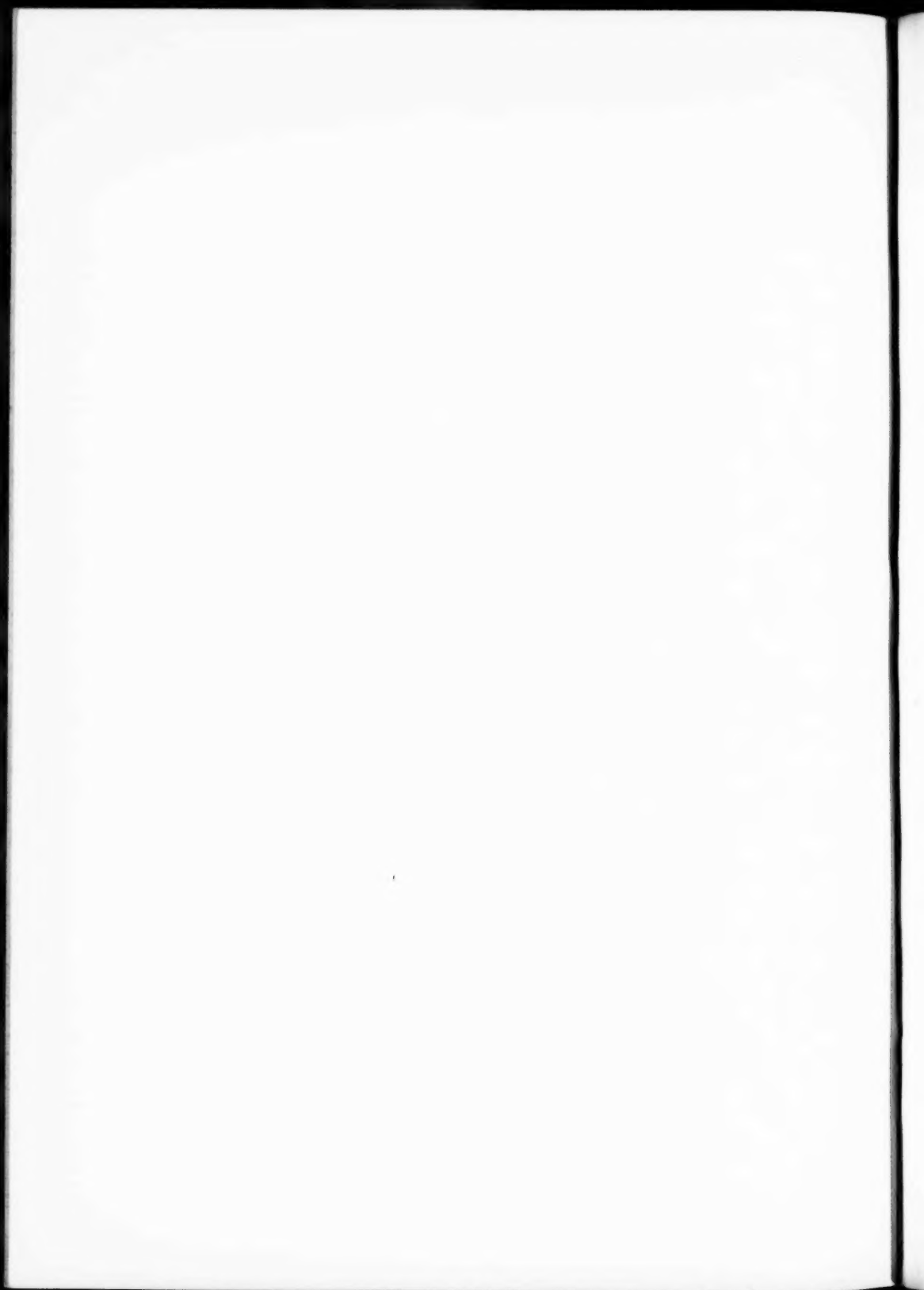
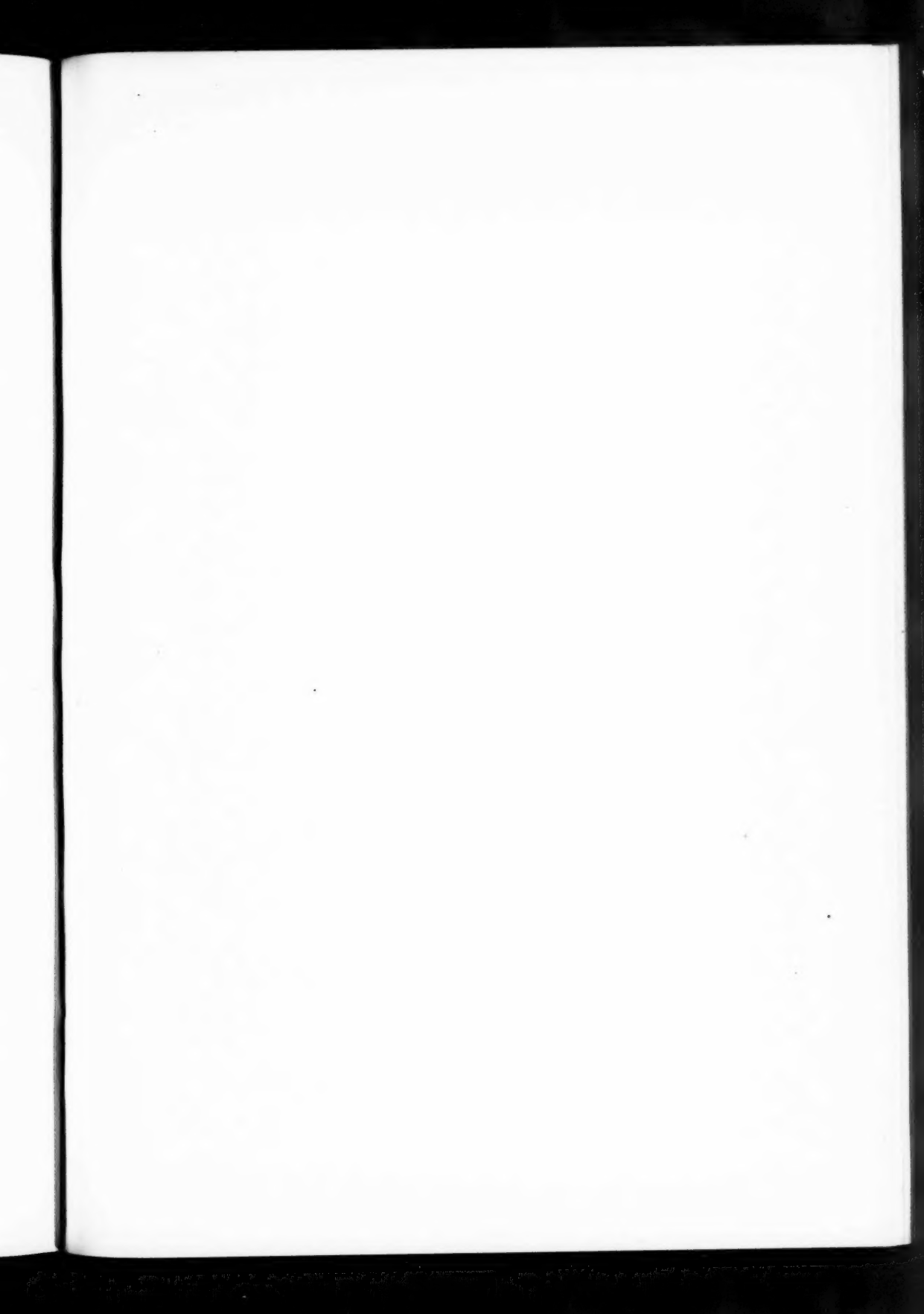


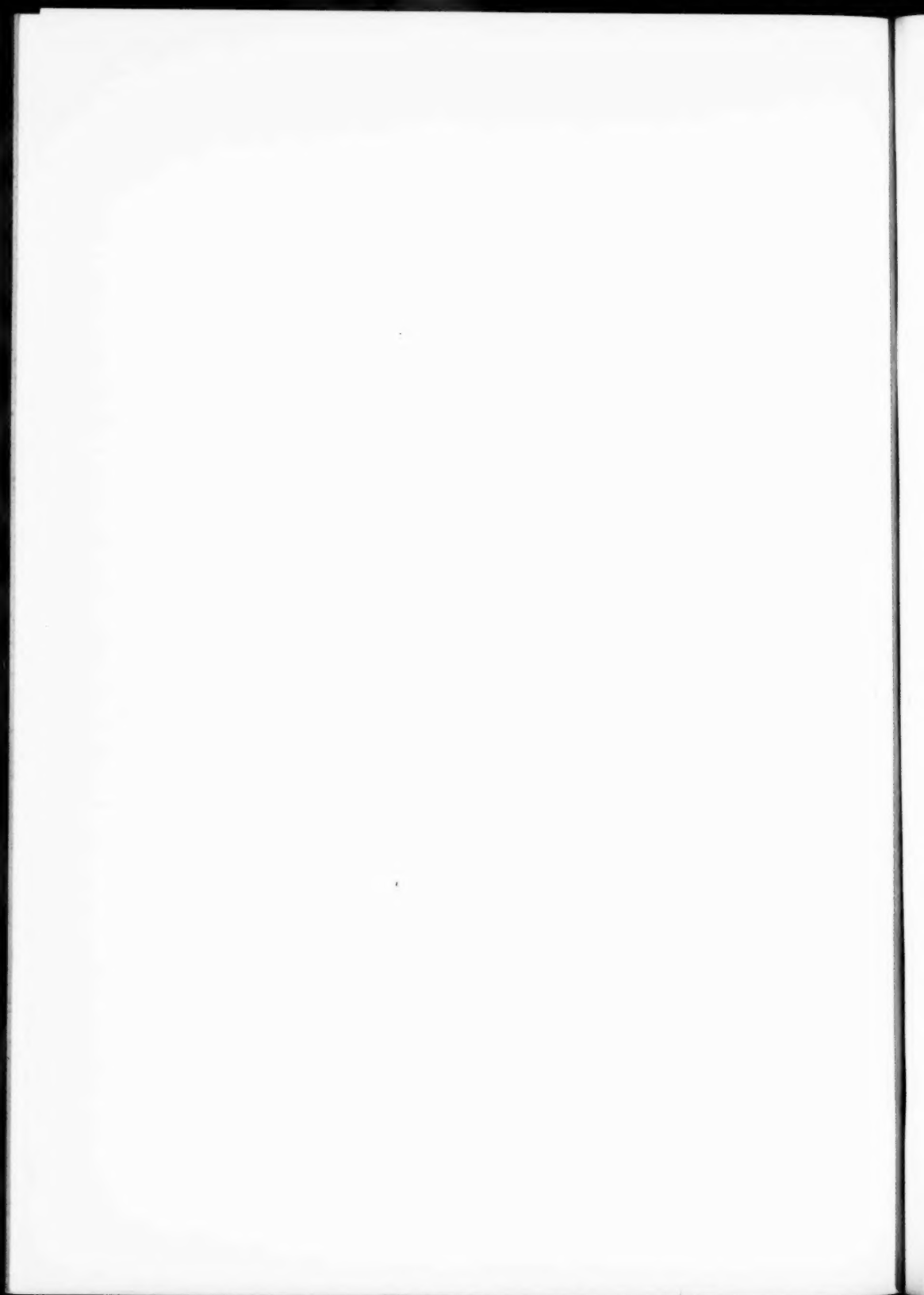
FIG. 1.



FIG. 2.







NEW FOSSIL PIG REMAINS FROM THE VAAL RIVER
GRAVELS.

By J. C. MIDDLETON SHAW, Department of Dentistry, and H. B. S.
COOKE, Department of Geology, University of the Witwatersrand,
Johannesburg.

(With Plate LIV and one Text-figure.)

(Read March 20, 1940.)

INTRODUCTION.

The joint geological and archaeological survey of the Vaal River basin (Söhnge, Visser, and Lowe, 1937) resulted in the discovery of a large number of fossilised mammalian teeth and bones. These remains were placed at the disposal of one of the authors (H. B. S. C.) for examination and description, and will be reported on in papers and a memoir.

The present paper deals with a number of teeth in the collection which have been ascribed to three new fossil representatives of the family *Suidae*. The other author (J. C. M. S.) has recently investigated and described (1938, 1939) a large collection of teeth of living and fossil members of this family. The authors decided, therefore, to collaborate in investigating and reporting on the pig material which has now become available.

DESCRIPTION.

Mesochoerus (gen. nov.) *paiceae* (Broom).

(Plate LIV, figs. 1 and 2.)

1931. *Notochoerus paiceae* Broom, Rec. Alb. Mus., IV, i, pp. 167-168, fig. 1.

The new material is a left half of a mandible lacking the anterior and posterior portions through fracture, and having *in situ* the roots of a second premolar, damaged third and fourth premolars, a much damaged first molar and very well-preserved second and third molars.

The third molar is the most interesting and important tooth in the jaw, and the bone has therefore been cleared away leaving the specimen completely exposed. The tooth is almost fully erupted, and its occlusal surface lies in the same occlusal plane as the corresponding surfaces of the second molar. The surface is, however, completely unworn, and this can only

be explained by the assumption that the corresponding tooth of the upper jaw had not erupted into a position of occlusion.

The principal dimensions of the third molar are as follows:—

Greatest antero-posterior length	68 mm.
Width across anterior group of columns	22 mm.
Height of anterior group of columns with roots	45 mm.
Height of anterior group of columns excluding roots	34 mm.
Height of posterior group of columns excluding roots	31 mm.

The crown is made up of four pairs of lateral columns and seven median columns, the first and last of the median columns occupying the anterior and posterior extremities respectively. The columns are all of much the same height (approximately 32 mm.) and at the base of the lateral columns there is a pronounced cingulum. The lateral columns terminate by means of roots, which are strongly developed on the first and second pair of columns.

In 1931 Broom described the type third molar, which has very similar characters and which was found in the Vaal River diamond gravels at Windsorton. This tooth measures 70.0 mm. in length and 22.5 mm. in width. It is severely abraded on its occlusal surface, but from the form of the columns on this surface it can be concluded that prior to wear the characters of the tooth were identical with those of the tooth now discovered. Broom (1931) provisionally placed the pig represented by this tooth in the genus *Notochoerus* and established for it a new species, *Notochoerus paiceae*. He stated, however, that it "probably will later have to be placed in a distinct genus."

Now that an unworn third molar and other teeth of this pig have been discovered, there seems no doubt that Broom's latter view is correct. The third molars of this new pig differ from *Notochoerus* third molars in several important respects. They are considerably less hypsodont. They have columns which are clearly separated from one another, and a cingulum which demarcates the junction of the columns with the roots. Moreover, the roots are larger than in *Notochoerus* third molars and, unlike the latter, they are of the brachyodont type. The premolar and first and second molars have been compared with corresponding teeth in a lower jaw of *Notochoerus* which Dr. Broom has kindly placed at the authors' disposal. Like the third molar, these teeth differ markedly from corresponding teeth of the *Notochoerus* type. They confirm the view of Broom and the present authors that the pig is not *Notochoerus*.

It seems possible that the new pig has affinities with the forest-pig *Hylochoerus*. Living forms of *Hylochoerus* have been discovered in Central Africa (Thomas, 1904) and in North Africa, and fossil forms of this genus

have been found in East Africa and described by Hopwood (1926, 1931). In the genotype of *Hylochoerus* the length of the lower third molar is 41 mm., which is considerably less than in either Broom's or the present authors' specimens. In other respects also there are important differences, such as the tendency of the *Hylochoerus* molar to brachyodontism. Nevertheless, in general appearance the *Hylochoerus* third molars call to mind the teeth discovered in the Vaal. In *Hylochoerus* the premolar teeth are reduced both in size and number when compared with the corresponding teeth in the authors' jaw. The first molar of the new fossil is too damaged for comparative purposes, but the second molar has characters which resemble those of second molars of *Hylochoerus*. The fossil second molar has a length of 31 mm., as compared with 26.5 mm. in the genotype of *Hylochoerus*.

There is no doubt that the pig represented by the new fossil jaw and by Dr. Broom's third molar has closer affinities to *Hylochoerus* than to *Notochoerus*. *Hylochoerus* is, however, a highly specialised type of pig, and the reduction in size and number of its premolars, coupled with characters found in its third molars, clearly distinguishes it from the pig represented by the fossil material from the Vaal. It is apparent, in fact, that the fossil material represents a new genus of pig.

The authors propose for this new genus the name *Mesochocerus*. Broom's specific name (*paiceae*) must be retained and the new specimen may be regarded as a neotype of *Mesochocerus paiceae* (Broom).

Notochoerus broomi sp. nov.

(Text-fig. 1.)

The type is a lower third molar of a young individual (fig. 1). It lacks, through injury, two or more columns at its posterior end, and all the columns are slightly shortened by damage at the base. The following are the principal dimensions of the specimen:—

Greatest antero-posterior length (as preserved)	. 32 mm.
Width of anterior group of columns	. 15.5 mm.
Height of second lateral column	. 42 mm.

As preserved, the specimen presents three pairs of lateral columns and four median columns. The first median column is stoutly developed and occupies the anterior extremity. The specimen is of the hypsodont type, and from the form of its columns both on their lateral and occlusal aspects it is apparent that it represents a form of *Notochoerus*. As will be seen, however, from the dimensions given above, it is a considerably smaller tooth than any *Notochoerus* teeth hitherto described. It seems probable, in fact, that it represents a dwarf species of *Notochoerus*. As



FIG. 1.—Type lower third molar of *Notochoerus broomi* Shaw and Cooke. Enamel pattern (above) and lateral view (below) showing possible restoration. Natural size. (Bureau of Archaeology Fossil Coll., No. 35.)

the genus *Notochoerus* was originally founded by Dr. Broom, it is proposed to distinguish the species now identified as *Notochoerus broomi* sp. nov.

Phacochoerus altidens sp. nov.

(Plate LIV, figs. 3 and 4.)

The material is a third molar, which is broken at its anterior end and also at its base. It is fairly well worn, of the phacochere type, and presents the uncommon condition of four, and in a few situations five, rows of columns.

As preserved, this specimen is markedly larger than any third molar of this type hitherto described. The following are its present principal dimensions:—

Greatest height (from base to occlusal surface)	. 81 mm.
Greatest antero-posterior length	. . . 64 mm.
Length on occlusal surface	. . . 41 mm.
Greatest width at occlusal surface	. . . 18.5 mm.

Prior to injury, the estimated corresponding dimensions were:

Greatest height	. . . 86 mm.
Greatest antero-posterior length	. . . 75 mm.
Length on occlusal surface	. . . 73 mm.
Greatest width at occlusal surface	. . . 19.3 mm.

The largest tooth in an extensive collection of modern and fossilised phacochere third molars assembled by one of the authors has the following dimensions:—

Greatest height	70 mm.
Greatest antero-posterior length	58 mm.
Length on occlusal surface	52 mm.
Greatest width at occlusal surface	15.5 mm.

The largest tooth of this type, in Van Hoepen's collection, measured:

Greatest height	76 mm.
Length on occlusal surface	49 mm.
Greatest width at occlusal surface	15 mm.

Van Hoepen (1932) regarded the latter tooth as representing a new genus and species, *Stylochoerus compactus*, but, notwithstanding its large size, it was considered (Shaw, 1939) that it could represent either *Phacochoerus africanus* or *P. aethiopicus*, probably the latter.

Obviously, however, some limit must be set to the degree in which teeth can vary in size in the same species. The average dimensions of a fully developed *P. africanus* or *P. aethiopicus* third molar are:

Greatest height	52 mm.
Length on occlusal surface	49 mm.
Greatest width at occlusal surface	12 mm.

Van Hoepen's large specimen, although 24 mm. higher, is much the same length and only slightly wider than the average tooth of this type. Prior to injury, the present specimen must have been at least 30 mm. higher, 26 mm. longer, and 7 mm. wider than the average.

In view of these facts it would be unwarranted to regard the specimen as representing either *P. africanus* or *P. aethiopicus*. The presence of more than the normal number of three rows of columns might be considered to indicate that the pig represented by the specimen should be removed from the genus *Phacochoerus*. It has been shown, however, in another report (Shaw, 1939) that more than three rows of columns are found in living phacocheres. There is, therefore, no necessity to remove this new pig from the genus *Phacochoerus*. There is no doubt, however, that the animal requires specific designation and the authors propose the name *Phacochoerus altidens* sp. nov.

LOCALITIES AND GEOLOGICAL HORIZONS.

The mandible was recovered from dumps of material excavated by diggers on the Pniel Estate, opposite Barkley West and on the left bank of the Vaal River. The gravels being worked belong to the group of terrace deposits named the Younger Gravels in the Vaal River survey

(1937), but it cannot be stated with certainty from what part of the deposits the specimen was derived. The ferruginised sand adhering to and filling the cracks and hollows in the mandible suggest that it originally lay on, rather than in, the gravel and was covered by the sand which normally overlies the gravel. Fossilisation is not complete, though the bone is well impregnated, and this supports the idea of its situation on the gravels. It can be stated, however, that the specimen is not older than the middle or second phase of the Younger Gravels. In all probability it belongs to the third phase of the Younger Gravels.

The locality and horizon of derivation of the molar of *Notochoerus broomi* is unfortunately not recorded, but the tooth bears the typical encrustation of the material from the Younger Gravels and is completely fossilised. It is probable that it belongs to some phase of those deposits.

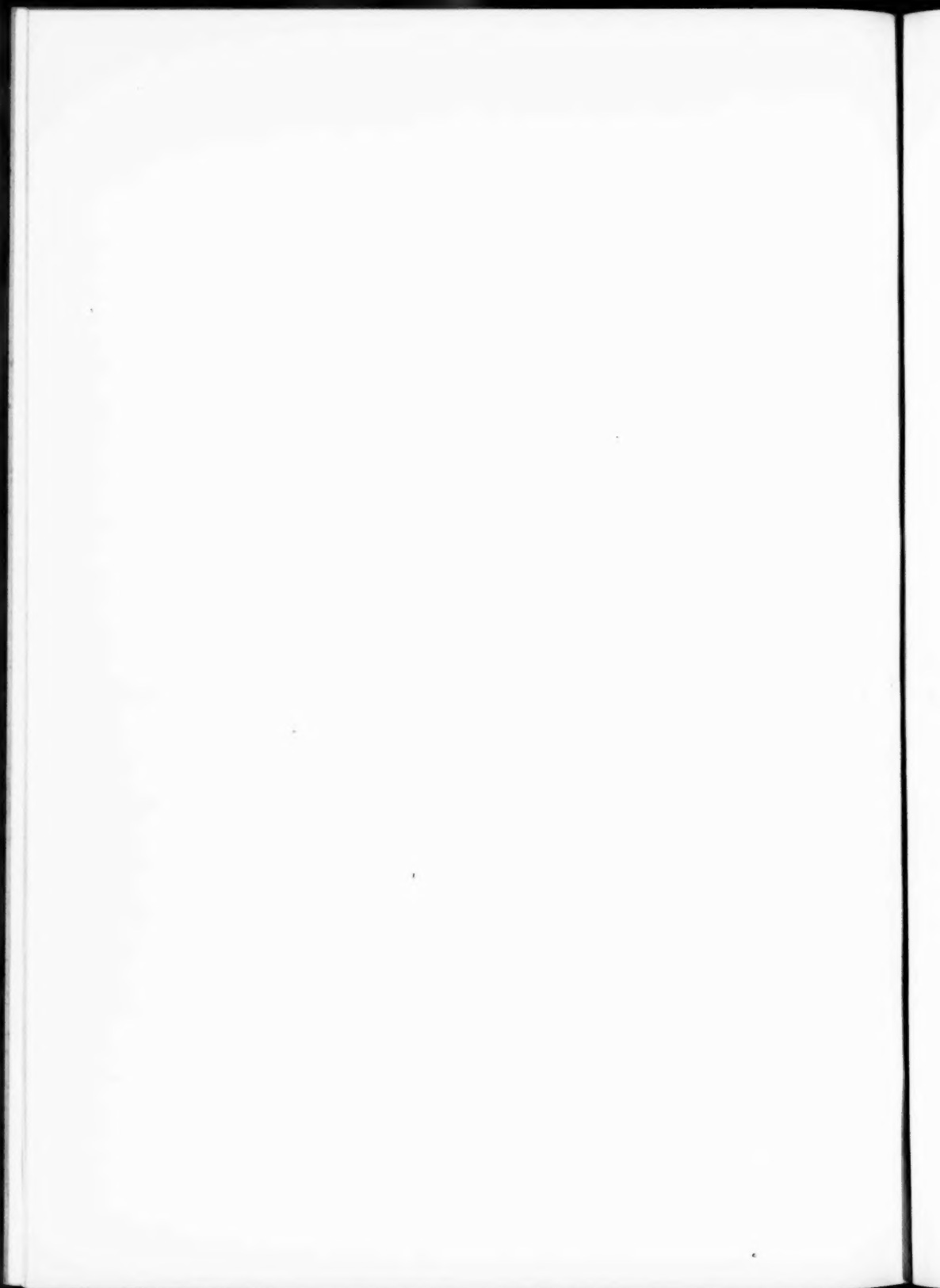
The loose phacochere molar is more precisely recorded as coming from Larsen's pits at Riverview Estate, near Windsorton. Larsen was working in gravels belonging to the middle phase of deposition of the Younger Gravels, so that the horizon from which the specimen comes is defined within fairly narrow limits. The degree of fossilisation is in agreement with such a position so far as it can be judged. It may be added that Broom's specimen of *Meschoerus paiceae* was recovered from the diamond gravels at Windsorton and that its age is probably also middle Younger Gravel.

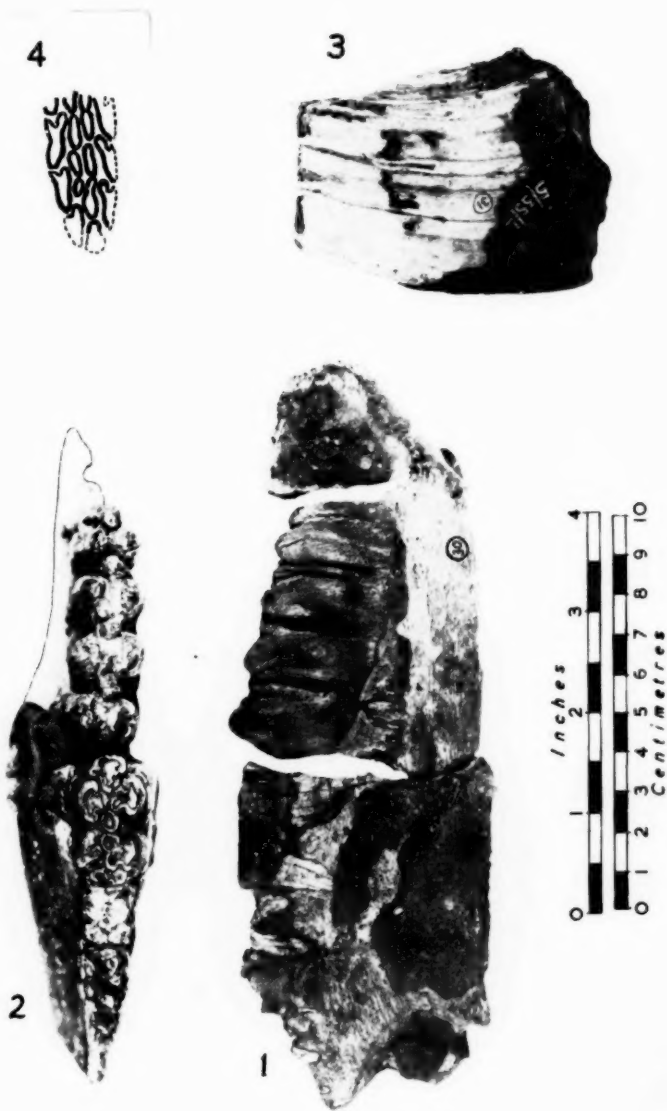
BIBLIOGRAPHY.

- BROOM, R., 1931. "A new Extinct Giant Pig from the Diamond Gravels of Windsorton, South Africa," *Rec. Albany Mus.*, IV, i, pp. 167-168.
- BROOM, R., 1936. "New Pleistocene Mammals from Limestone Caves of the Transvaal," *S. Afr. J. Sci.*, xxxiii, pp. 750-768.
- HOPWOOD, A. T., 1926. "Mammalia" in the "Geology and Palaeontology of the Kaiso Bone Beds," *Occ. Paper, No. 2, Geological Survey of Uganda*.
- HOPWOOD, A. T., 1931. "Preliminary Report on the Fossil Mammalia." Appendix C to L. S. B. Leakey, "The Stone Age Cultures of Kenya Colony." Cambridge Univ. Press.
- SHAW, J. C. M., 1938. "The Teeth of the South African Fossil Pig (*Notochoerus capensis* syn. *meadowsi*) and their Geological Significance," *Trans. Roy. Soc. S.A.*, xxvi, pp. 25-37.
- SHAW, J. C. M., 1939. "Growth Changes and Variations in Warthog Third Molars and their Palaeontological Importance," *Trans. Roy. Soc. S.A.*, xxvii, pp. 51-94.
- SÖHNGE, P. C., VISSER, D. J. L., and VAN RIET LOWE, C., 1937. "The Geology and Archaeology of the Vaal River Basin," *Memoir, No. 35, Geol. Survey, Union of S.A.*, pp. 1-164.
- THOMAS, O., 1904. "On *Hylochoerus*, the Forest-Pig of Central Africa," *Proc. Zool. Soc. Lond.*, 1904, ii, pp. 193-199.
- VAN HOEPEN, E. C. N., 1932. "Vrystaatse Wilde Varke," *Pal. Nav. Nas. Mus. Bloemfontein*, ii, p. 4.

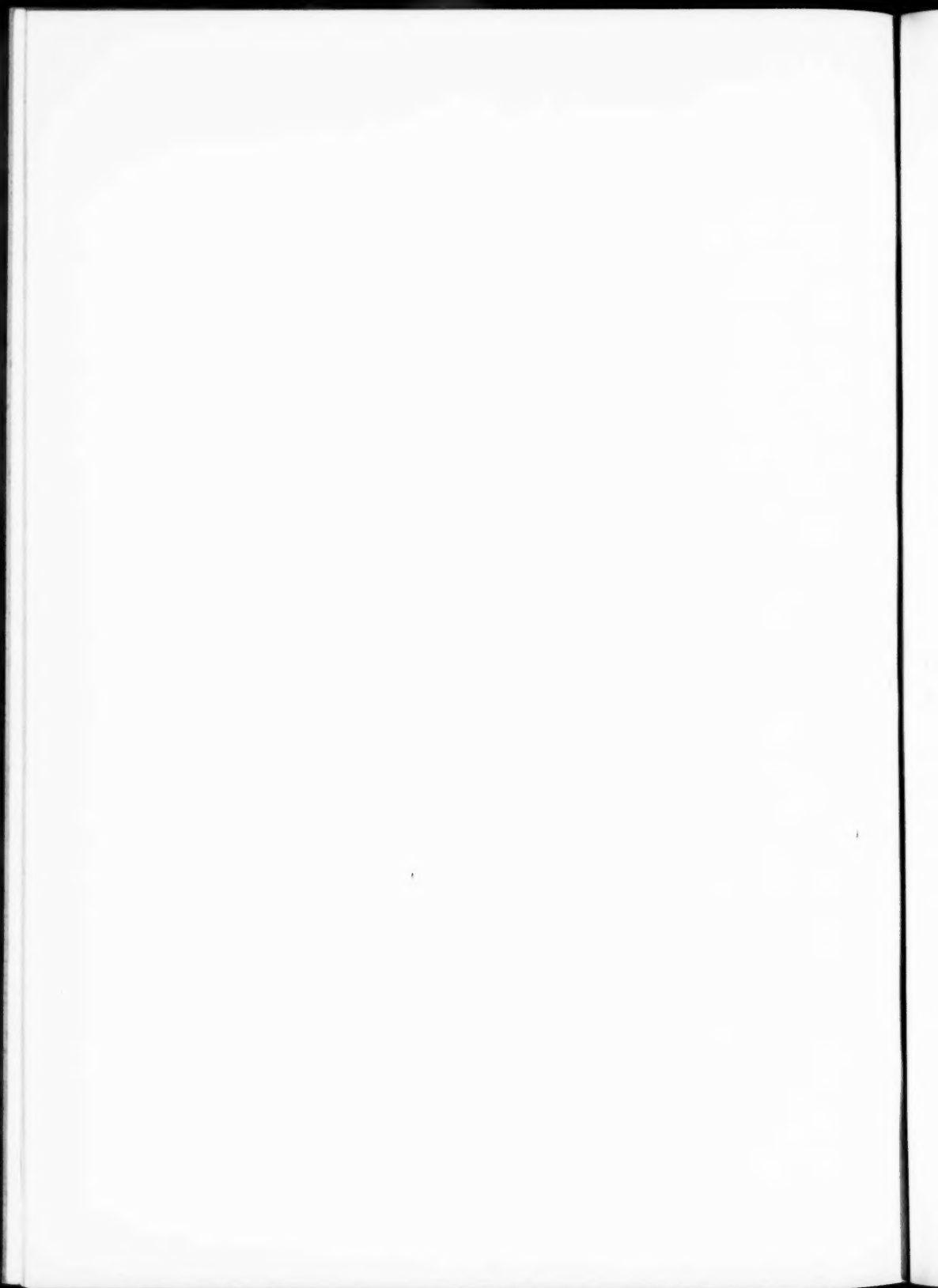
EXPLANATION OF PLATE.

- Fig. 1. Outer lateral view of left mandible of the neotype of *Mesochorus paiceae* (Broom)
(Bureau of Archaeology Fossil Coll., No. 30).
Fig. 2. Occlusal view of left mandible of *M. paiceae*.
Fig. 3. Lateral view of posterior portion of type third molar of *Phacochoerus altidens*
Shaw and Cooke (Bureau of Archaeology Fossil Coll., No. 31).
Fig. 4. Enamel pattern of posterior portion of occlusal surface of *P. altidens*.





[Photo: W. Paff.]



A FOSSIL HORSE FROM KOFFIEFONTEIN, O.F.S.

By L. H. WELLS, Lecturer in Anatomy, University of the
Witwatersrand, Johannesburg.

(With Plate LV and one Text-figure.)

(Read May 15, 1940.)

The fossil equine remains discussed in this paper were presented to the Department of Anatomy, University of the Witwatersrand, in 1930 by Mr. W. Fowler of Koffiefontein. As a preliminary study left some doubts as to their identification, especially in view of the observations of Haughton (1932), they have remained undescribed up to the present time. The writer's interest in them has, however, been revived as the result of discussion with Mr. H. B. S. Cooke, who is examining the equine and other fossils collected during the Geological and Archaeological Survey of the Vaal River Gravels. These discussions have lent support to the writer's original views on the specific distinctness of this material. In any case, its excellent preservation and unusually complete nature have been deemed to warrant an adequate record.

Of these remains, the most important are a series of skull fragments, found together at a depth of about 18 inches in surface soil overlying shale. These include the greater part of the right maxilla and palatine bone, with Pm^2 - M^3 in position and perfectly preserved, the right premaxilla containing an unerupted I^3 , and part of the left maxilla lacking teeth (Pl. LV). The remains are those of an individual not quite fully grown, I^3 being unerupted and M^3 only partially so. Pm^1 had been shed some time before death, its alveolus being partially obliterated; I^1 , I^2 , and C have been lost after death. The presence of the socket for C suggests that the individual is a male. Fine brownish-grey soil is present in the cavities of the bones, which are appreciably mineralised.

These fragments belong to an individual of large size; the total length of the upper jaw was about 44.5 cm., and the breadth across the first molars 16.5 cm., dimensions exceeding those of many specimens of *E. caballus*. The length of Pm^2 - M^3 is 20.6 cm., while the diastema between Pm^2 and I^3 measured approximately 11 cm. Pl. LV, C, shows the marked hollowing of the lateral aspect of the maxilla in its upper portion, below

the naso-maxillary suture. This region thus presented a form seen in the asses and in the quagga group, but not in the caballine horses nor, to any marked degree, in the mountain zebra.

In correspondence with the size of the skull, the teeth are large, as is shown by the following table:—

Tooth.	Height.		Length.	Breadth.	Length of protocone.
	Including roots.	Excluding roots.			
Pm ²	70 mm.	56 mm.	44 mm.	29 mm.	13.0 mm.
Pm ³	76 mm.	66 mm.	35 mm.	31 mm.	14.5 mm.
Pm ⁴	79 mm.	70 mm.	32 mm.	31 mm.	15.0 mm.
M ¹	76 mm.	64 mm.	32 mm.	30 mm.	13.5 mm.
M ²	82 mm.	74 mm.	33 mm.	29 mm.	15.0 mm.
M ³	78 mm. +	76 mm.	32 mm.	24 mm.	15.0 mm.

The fact that in Pm³-M² the length of the crown exceeds its breadth may be regarded as a consequence of the youth of the specimen.

The enamel pattern of the teeth (fig. 1, A) conforms generally to the characters of the "quagga group" of Haughton, to which this animal clearly belongs. On the outer side, the halves of the ectoloph are deeply concave. The parastyle and mesostyle are prominent and massive, especially in the premolars, and are more or less conspicuously grooved. As the table shows, the protocone is consistently elongated; its connection with the protoloph is established very near its anterior extremity, so that the elongation appears to affect chiefly the posterior lobe. The medial wall of the protocone is sinuous, with an ill-defined median groove. In Pm³ and Pm⁴ the protocone has a very oblique direction. These two teeth also show a remarkable prominence of the hypostyle, while in Pm² the "talon" is deflected medially. There is one strongly developed caballine fold in all the teeth (duplicated in Pm² and Pm³), and a rudimentary second fold.

On the walls of the fossettes the enamel is irregularly crimped, and its secondary plications are numerous but relatively coarse. The protoloph and hypostyle folds are strongly developed except in M¹, and may be reduplicated; in Pm² the protoloph fold is united to the ectoloph, cutting off the anterior extremity of the pre-fossette. Even in M¹ the protoconule fold is duplicated, and in some of the other teeth it attains a very complex development. The post-fossette folds show a similar elaboration, but the pre-fossette folds are less complex, being single in Pm² and M¹.

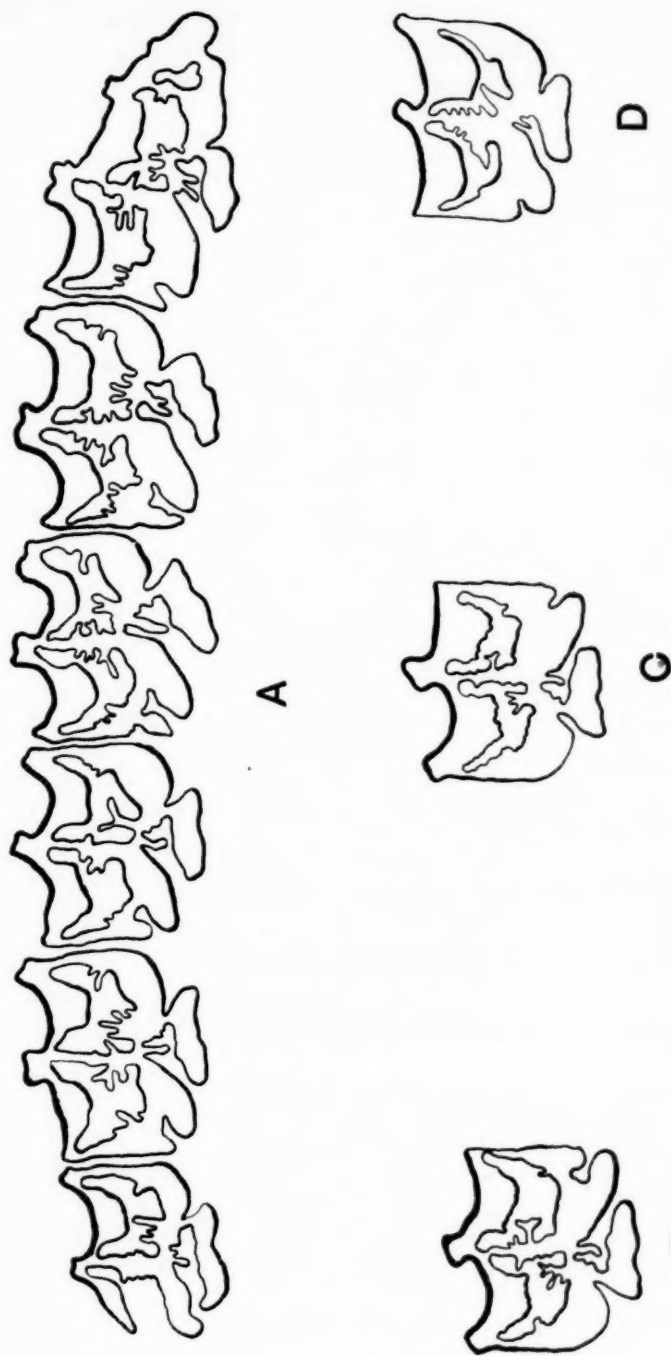


FIG. 1. A. Crown pattern of right upper cheek teeth of skull; B. Crown pattern of isolated left M_1 ; C. Pattern on section of crown of isolated left M_1 ; D. Crown pattern of isolated right M_2 (M.M.K. 4342). Natural size.

Mr. Fowler also presented an isolated left first upper molar, found half a mile distant from the skull fragments and at a depth of 5 feet in similar soil. Although the state of preservation of this tooth is appreciably different from that of the skull, it clearly belongs to the same species. The tooth is that of a relatively young individual. Its total height is 76 mm. (excluding the roots 65 mm.); the crown is 32 mm. long by 30 mm. broad, and the protocone measures 15 mm. These dimensions correspond closely with those of M^1 in the skull. The tooth is only slightly curved. Its crown pattern (fig. 1, B) also corresponds closely with that of M^1 in the skull, except that the minor plications are more developed.

A section has been made through the crown of this tooth 15–20 mm. below the grinding surface (fig. 1, C). At this level the crown is 30 mm. long by 30 mm. broad, and the protocone 14 mm. in length. The minor enamel plications are reduced in size, but all are still distinct, the protoconule and post-fossette folds being multiple. The inlet between hypocone and hypostyle is reduced; it remains visible, however, down to the commencement of the roots.

The general characters of these remains show that they belong to a large representative of the "quagga group," appreciably exceeding in size the living members of that group. Of the known fossil types conforming to this general description, the upper teeth assigned by Houghton to *E. capensis* Broom are sharply differentiated from the material under discussion by the simplicity of their enamel pattern. *E. cawoodi* Broom affords a much closer comparison, and the ascription of these remains to that species has been very seriously considered. However, typical teeth of *E. cawoodi* are somewhat larger than those described in this paper, the posterior lobe of the protocone is not so strongly developed, nor are the minor enamel folds so complex. The elaboration of the protoconule fold in both the individuals included in the present material is especially distinctive. In view of the limitations of our present knowledge of *E. cawoodi*, it is thus doubtful whether these specimens can be assigned to that species. If Houghton is correct in including *E. helmei* Dreyer in *E. cawoodi*, the gap between that species and our material is rather increased than diminished.

In size and in the complexity of the enamel pattern this material makes some approach to the type of *E. kuhni* Broom. The enamel plications of that species are, however, much finer, and the character of the protocone widely different. Teeth intermediate in character between *E. cawoodi* and *E. kuhni* have been named by van Hoepen *E. louwi* (merged by Houghton in *E. kuhni*), but the present material does not compare very closely with these.

It appears justifiable, therefore, to create a new species for the reception

of these remains, while fully appreciating that more complete knowledge of the types already described may cause it to be merged in one of them. This species I propose to name in honour of Mr. Fowler, to whom we owe this excellent material.

Equus fowleri, sp. nov.

Type.—Portions of skull and isolated tooth catalogued as No. 555 in the collection of the Department of Anatomy, University of the Witwatersrand, Johannesburg.

Diagnosis.—Cheek teeth 28–32 mm. in breadth; halves of ectoloph concave: parastyle and mesostyle massive, prominent and grooved, particularly in premolars: great development of posterior lobe of protocone: deep and complex protoconule, pre-fossette and post fossette folds: strong (sometimes double) caballine fold.

Locality.—Koffiefontein, O.F.S.

The age of the specimen cannot be determined with certainty, but is most probably Late Pleistocene.

I wish to record my thanks to Dr. S. H. Haughton and to Mr. H. B. S. Cooke for their very valuable comments on the material and text of this report.

ADDENDUM.—After the foregoing description had been completed, Mr. H. B. S. Cooke received, through the kindness of Dr. Haughton, a collection of mammalian fossils which had been lying for some time at the South African Museum, Cape Town. Included among these are a number of equine and other remains from Koffiefontein, belonging to the McGregor Memorial Museum, Kimberley, to which they had been presented by Mr. Fowler. Of the equine specimens, one upper molar presents a close general resemblance to the material just described, and may provisionally be referred to *E. fowleri*. Mr. Cooke has allowed me to add to my paper a description of this specimen.

The tooth, numbered 4342 in the collection of the McGregor Museum, is a right M², complete except for the roots. Though differing somewhat in its state from the material previously described, it is also appreciably mineralised, and retains traces of similar brownish soil. It appears rather more worn than M² of the type skull; nevertheless its height without roots is 76 mm.; it is slightly curved. The crown is 29.5 mm. long by 28.5 mm. broad, being thus slightly smaller than that of M² of the type-specimen, while the length of the protocone is 14 mm. Fig. 1, D, shows the general correspondence of the enamel pattern with that of the type, and even more with the section of the isolated M¹. Attention may be directed, however,

to the following differences: the parastyle and mesostyle are narrower, and very indistinctly grooved; the hypostyle is not prominent, and the inlet between it and the hypocone is relatively shallow, although it persists down to the root of the tooth; the crimping of the enamel is less conspicuous; the protoconule fold is single, though remarkably large. These differences cannot, however, be considered sufficient to exclude this specimen from *E. fowleri*.

It may be added that Mr. Cooke, in a forthcoming publication, advances cogent arguments for the view that *E. cawoodi* represents the upper dentition of *E. capensis*. The differences between the type of *E. cawoodi* and the upper molars hitherto assigned to *E. capensis* are considered by him to be essentially due to varying degrees of attrition. This interpretation appears to strengthen, rather than weaken, the arguments for the specific distinctness of *E. fowleri*.

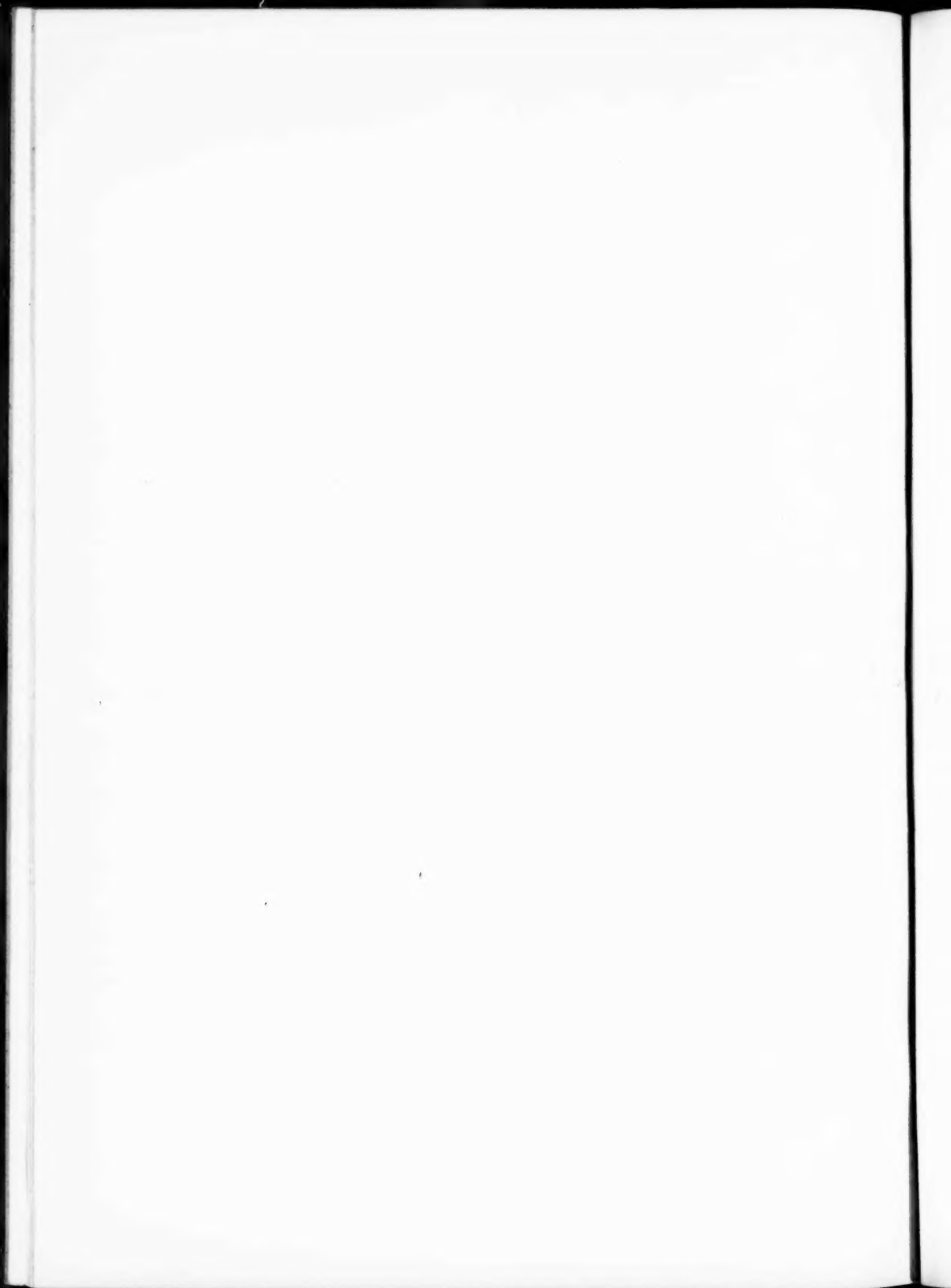
REFERENCE.

- HAUGHTON, S. H. (1932). "The Fossil Equidae of South Africa," Ann. S. Afr. Mus., vol. xxviii, pp. 407-427, illus.



FRAGMENTS OF SKULL OF FOSSIL HORSE FROM KOFFIEFONTEIN, O.F.S.

A. Lateral aspect of right maxilla and premaxilla; B. Palatal aspect of the same; C. Lateral aspect of left maxilla, showing excavation below naso-maxillary suture. One-half natural size.



THE COMPARATIVE ANATOMY OF THE TYMPANIC BULLA
AND AUDITORY OSSICLES, WITH A NOTE SUGGESTING
THEIR FUNCTION.

A Paper from the University of Cape Town.

J. A. KEEN.

(Department of Anatomy, University of Cape Town.)

C. S. GROBBELAAR.

(Zoological Institute, University of Stellenbosch.)

(With 78 Text-figures.)

(Read May 15, 1940.)

Although the tympanic bulla is such a striking element on the base of the skull in the majority of mammals, its function is not understood. In Weber's "Die Säugetiere" (1928) we find a statement that the bulla is perhaps a kind of resonance chamber, but beyond this the function is not discussed. In Winterstein's exhaustive work on comparative physiology (1913) the bulla is hardly mentioned, the whole discussion of sound conduction to the cochlea centering around the tympanic membrane and ossicles. Yet, this large air-space, which is an extension of the tympanic cavity, occurs so regularly in all smaller mammalian skulls, that it seems reasonable to make an attempt to link it up with the physiology of sound conduction, and to suggest that the tympanic bulla is a hearing adaptation.

The bulla is not a perfectly homologous structure in the mammals, as it may involve many different bony elements of the skull. The floor of the tympanic cavity is formed either by the petrous part of the os perioticum, or more often by the medial part of the os tympanicum; the latter has become applied to the petrous bone from below. The lateral part of the os tympanicum becomes drawn out to form the external auditory meatus. When the middle ear cavity extends and hollows out the neighbouring bones to form the tympanic bulla, the latter spreads well beyond the limits of the os tympanicum and os perioticum, and the following bony elements may share in its formation: in a forward direction the basi- and ali-sphenoid; posteriorly the exoccipital, and upwards the mastoid part of the os perioticum and the squamosal.

Embryologically the tympanic bulla must be formed by an outgrowth of the mucous membrane of the tympanic cavity, in the same way as the skull bones around the nasal cavities become hollowed-out to form the nasal air sinuses. As we know, this activity of the embryonic mucous membrane is never limited to individual bony elements, and the air cavity-forming process spreads freely across sutures. Therefore the multiplicity of the skull elements sharing in the formation of the bulla is in no way extraordinary.

Ever since zoologists and anatomists began to study the skull bones, the tympanic bulla has been recognized as an important feature in the architecture of the skull, and the literature on the morphology of the tympanic or auditory bulla is very extensive (van Kampen, Le Gros Clark, van der Klaauw). However, previous descriptions of mammalian skulls have not gone beyond stating whether the bulla in any particular species is large or small, whether it is a single air cavity or one with a partition, and also what skull bones take part in forming it.

Our aim has been not so much the study of the detailed morphology of the bulla in each species as such, but rather to compare the relative importance of the tympanic bullae in various species of the different mammalian orders. No such comparative survey seems to have been made before. We have chosen our material from the skulls which were available in the S.A. Museum, Cape Town, and we are therefore limited to some extent to mammalian species which are found in South Africa. In spite of this, we believe that the types chosen are fairly representative. Sketches of the posterior portion of the base of the skull have been made, the tympanic bulla or the petrous and tympanic bony elements being shown by special shading.

In order to demonstrate the relative importance of the bulla in each species, the skulls have been drawn to the same size approximately, *i.e.* the large skulls have been reduced and the small skulls enlarged. The degree of reduction and enlargement is made clear by the cm. scale which is placed underneath each sketch. In the various mammalian orders we have arranged the skulls according to size, beginning with the largest. This emphasizes at once one of the main features of the tympanic bulla, *viz.* that it occurs in the smaller animals and tends to be absent in the larger ones.

THE TYMPANIC BULLA (figs. 1-45).

Primates and Lemurs (figs. 1-6).—In the Primates the floor of the tympanic cavity is formed by the petrous part of the os perioticum, and in the lower members of this order (lemurs, tarsiers) the floor becomes distended to form the smooth rounded swelling of the tympanic bulla (Le

Gros Clark, 1934). There is no bulla in man and in the larger Primates (figs. 1-3). In the smaller monkeys one often sees the beginning of a bulge in the floor of the tympanic cavity. The bulge on the floor of the petrous bone in the Samango Monkey (fig. 4) was found to contain numerous small air cells, a condition usually described as a "cancellous" bulla. This is not a happily chosen term, as it leads to confusion with cancellous bone which contains red marrow.

Typical thin-walled bullae occur in the Lemurs (figs. 5 and 6). The floor of the tympanic cavity is inflated, the air cavity extending into the mastoid part of the os perioticum. If the egg-shell floor of the bulla is broken away the cochlea may be seen projecting into the cavity like a knob (fig. 5). The macroscopic appearance of the cochlea of Garnett's Lemur shows that this species has a flat type of cochlea with $2\frac{1}{2}$ turns. In the Moholi Lemur, with a total skull length of only 4 cm., the bulla occupies approximately one-third of the whole length of the base of skull (fig. 6).

Ungulates (figs. 7-16).—In the Ungulates the external auditory meatus is usually a well-formed, long and completely circular canal, which is part of the os tympanicum. However, in some of the suborders there is a so-called "pseudomeatus" (Weber, 1927), the outer part of the meatus being formed by a special adaptation of the postglenoid process of the squamosal in front and a downward projection of the mastoid part of the os perioticum behind. A "pseudomeatus" is seen typically in the Hippopotamus and Rhinoceros (figs. 9 and 10), and to a less extent in the Equidae (fig. 11). In the Elephant there is a comparatively small bulge in the floor of the tympanic cavity consisting of "cancellous" bone. The Buffalo, although a large animal, possesses a bulla which is divided into two parts by a partition. The Giraffe has a small, thick-walled bulla. Many of the large antelopes (Wildebeest, Kudu) have fairly well-marked bullae. In the Hippopotamus and Wart-hog one finds a small "cancellous" bulla; no bulla occurs in the Rhinoceros and Zebra. The typical, large and thin-walled bulla is seen in the small antelopes, *e.g.* Steenbok (fig. 15). The Dassie, although among the smallest Ungulates, has no bulla. The part of the base of skull formed by the os tympanicum is a flat area (fig. 16). One may connect this observation with the interesting classification of the animal in a suborder among the larger Ungulates.

Carnivores (figs. 17-26).—The series of sketches of Carnivore skulls are an illustration of the general rule that the tympanic bulla is a feature which is seen chiefly in the smaller animals. In the large skulls of the Sea Leopard and Tiger (figs. 17 and 18) the os tympanicum presents a flat surface or only a slight bulging. The Lion is an exception to the general rule and has a fairly well-developed bulla with the partition typical of the Felidae.

When the bulla is comparatively small, *e.g.* in the Hyaena (fig. 19), the bulge shows itself first in the posterior part of the os tympanicum. The well-marked, rounded bulla of the cat (fig. 23) is almost completely divided into two cavities by a partition of thin bone. This partition separates a large medial compartment of the bulla in which the promontory and round window are seen, from a smaller lateral compartment containing the tympanic ring and ossicles.

In the smaller Carnivores (Mongoose, Meerkat) the large eggshell-like bulla occupies more than half of the posterior part of the skull base (figs. 25 and 26). An additional feature in these smaller Carnivores is a deficient ossification of the floor of the bulla. A part of the os tympanicum has failed to ossify, and in the dried and cleaned specimen there appear to be large openings into the bulla. In the Mongoose the opening is in the floor of the bulla (fig. 25), in the Meerkat the floor of the external auditory meatus is also deficient (fig. 26).

Rodents (figs. 27-35).—The Rodents are an order consisting of small animals with moderately large representatives (*e.g.* Hystrix). Possibly for that reason the tympanic bullae appear fairly uniform. But again the very small Rodents are those with bullae which occupy practically the whole of the posterior part of the skull base (figs. 30, 32, 33, 34 and 35). In many of the skulls there is a pointed process which serves to prolong the bony part of the Eustachian tube (figs. 27, 29, 30 and 31). This process has been given the special name of *processus styliformis* by van Kampen (1905). Another peculiarity of the Rodent skull is a bony bridge which unites the pterygoid hamulus with the bulla (figs. 27, 29, 30, 32 and 35). In the Rodents the bulla is said to be formed by the os tympanicum alone, in this respect resembling the Ungulates (van Kampen, 1905).

In the Guinea-pig and the Namaqualand Gerbille the right and left bullae respectively have been dissected by removing the thin bony floor in order to show the cochleae projecting freely into the air-space of the tympanic bulla (figs. 31 and 34). The $4\frac{1}{2}$ turns of the Guinea-pig's cochlea and the 4 turns of the Gerbillé's cochlea can be counted without difficulty. The sharp-pointed Guinea-pig's cochlea is $4\frac{1}{2}$ –5 mm. long from base to tip, that of the Gerbille about $3\frac{1}{2}$ mm.; the latter cochlea is flatter and correspondingly broader at the base. When van Kampen, in speaking of the Guinea-pig, says that "die Spitze des Promontoriums ragt frei hervor," he is clearly making a mistake. The "point" to which he refers is the extreme end of the cochlea and not the promontory, as can be seen in microscopic sections (fig. 46).

Insectivores (figs. 36-40).—The Insectivores are also an order of small mammals and some of the most inflated bullae are found among them. In Tenrec the bulla is not ossified below. The floor has either remained

TYMPANIC BULLA.

PRIMATES AND LEMURS.



FIG. 1.—*Homo sapiens*.

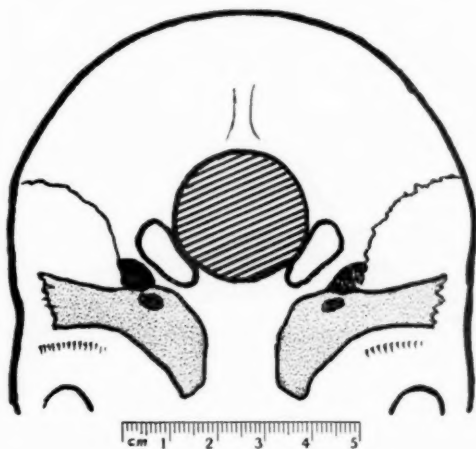


FIG. 2.—*Gorilla*.

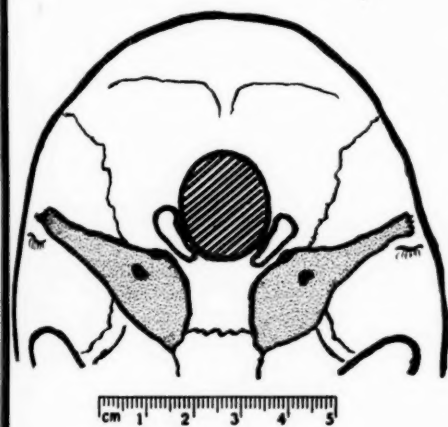


FIG. 3.—*Papio comatus*: Baboon.

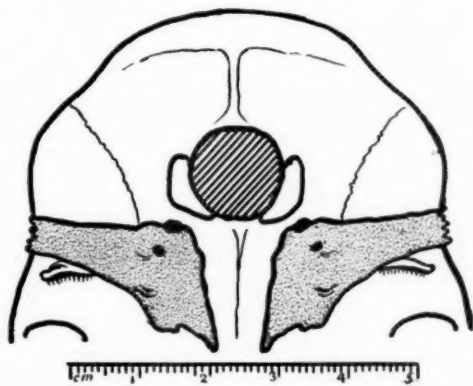
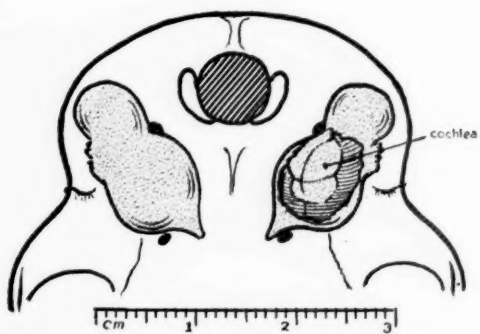
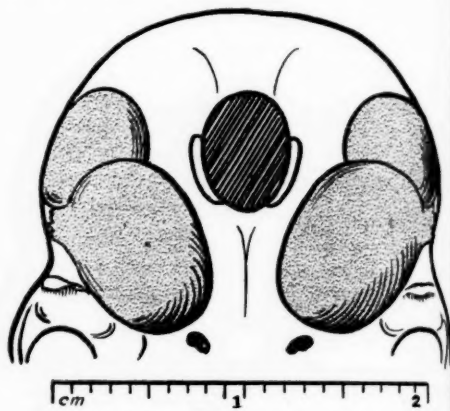


FIG. 4.—*Cercopithecus labiatus*: Samango Monkey.

FIG. 5.—*Otlemur garnetti*: Garnett's Lemur.FIG. 6.—*Galago senegalensis moholi*: Moholi Lemur.

UNGULATES.

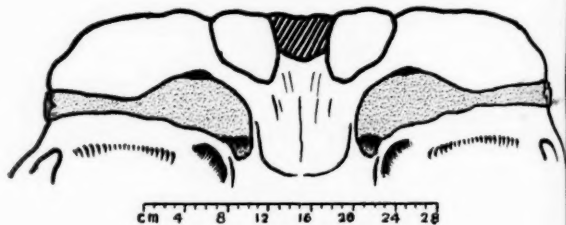
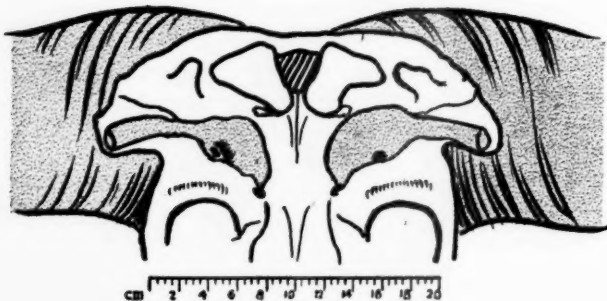


FIG. 7.—African Elephant.

FIG. 8.—*Syncerus caffer*: Buffalo.

TYMPANIC BULLA.

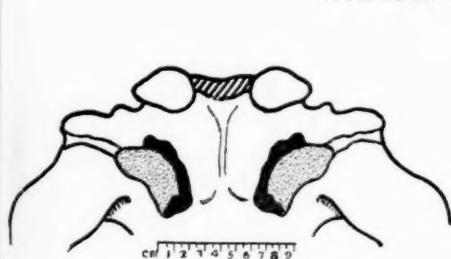


FIG. 9.—Hippopotamus.

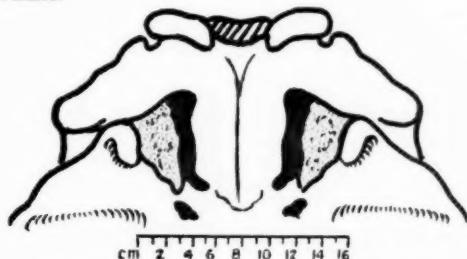


FIG. 10.—*Dicerus bicornis*: Black Rhinoceros.

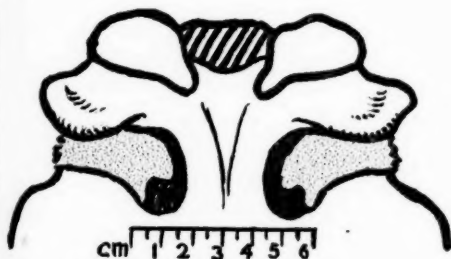


FIG. 11.—*Quagga quagga*: Zebra.

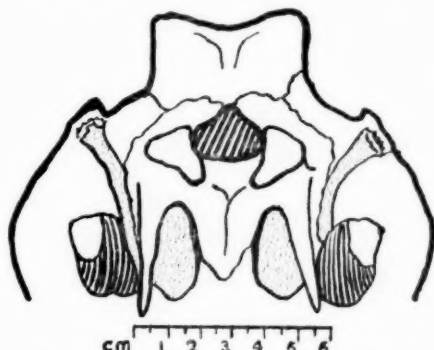


FIG. 12.—*Phacochoerus aethiopicus*: Wart-hog.

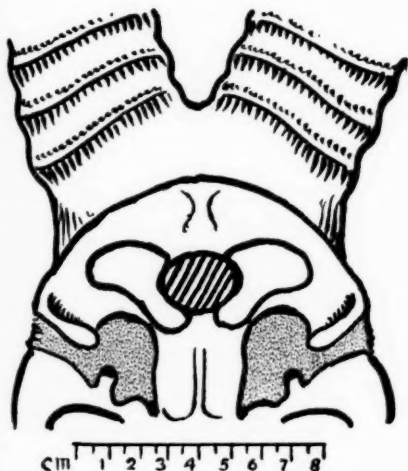


FIG. 13.—*Alcelaphus caama*: Red Hartebeest.

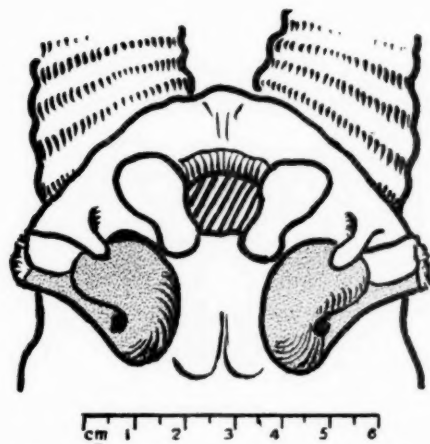
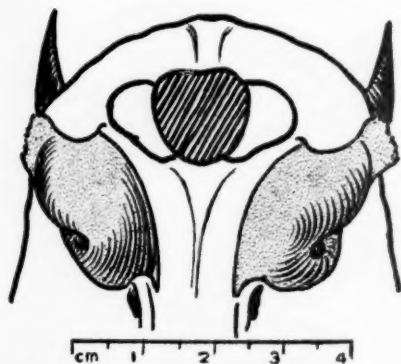
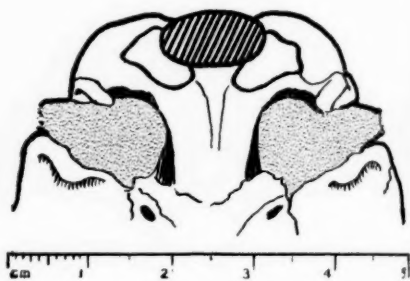
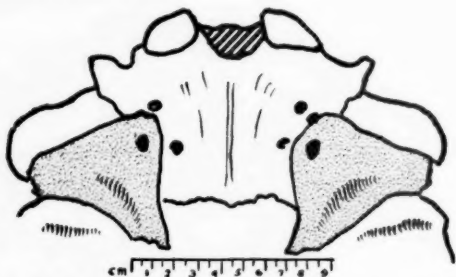
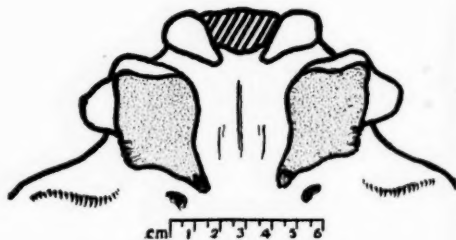
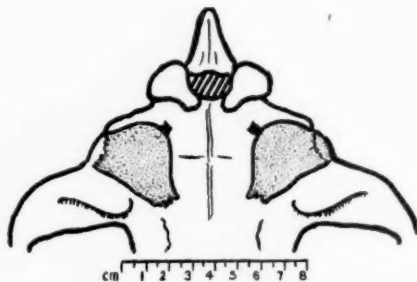
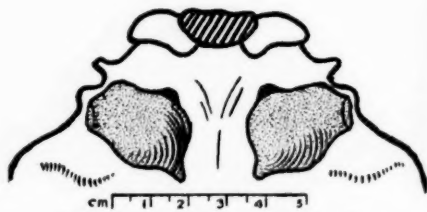


FIG. 14.—*Antidorcas marsupialis*: Springbuck.

FIG. 15.—*Raphiceros campestris*: Steenbok.FIG. 16.—*Procavia capensis*: Dassie.

CARNIVORES.

FIG. 17.—*Stenorhynchus leptonyx*: Sea Leopard.FIG. 18.—*Felis tigris*: Tiger.FIG. 19.—*Crocuta crocuta*: Hyaena.FIG. 20.—*Lycaon pictus*: Hunting Dog.

TYMPANIC BULLA.

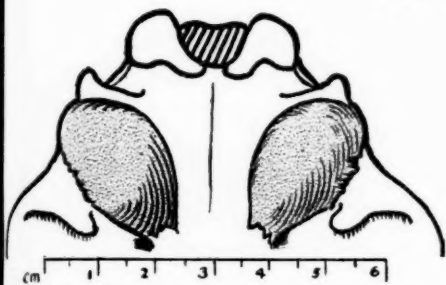


FIG. 21.—*Canis mesomelas*: Jackal.

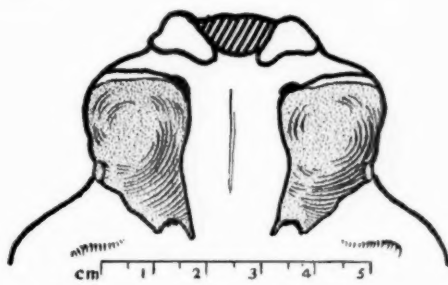


FIG. 22.—*Proteles cristatus*: Aard Wolf.

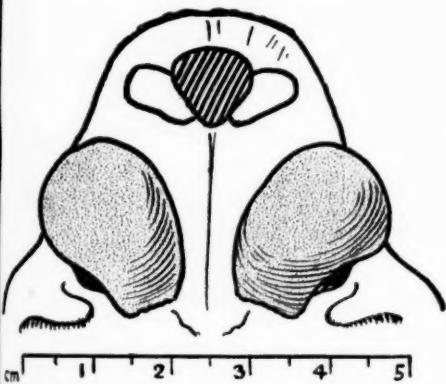


FIG. 23.—*Felis ocreata*: Wild Cat.

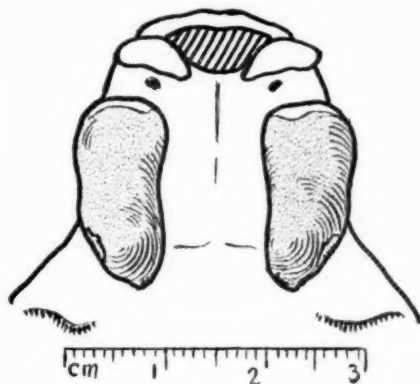


FIG. 24.—*Genetta felina*: Genet.

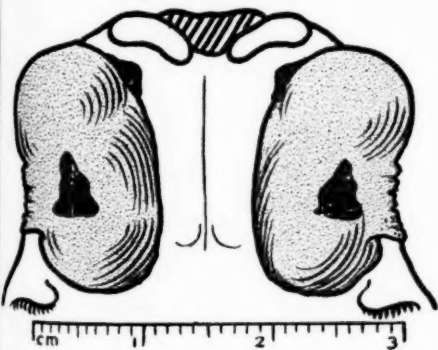


FIG. 25.—*Myonax pulverulentus*: Small Grey Mongoose.

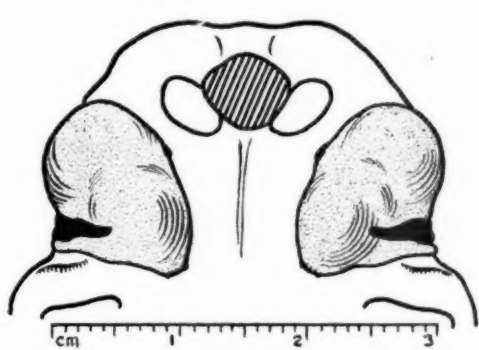


FIG. 26.—*Suricata suricatta*: Meerkat.

RODENTS.

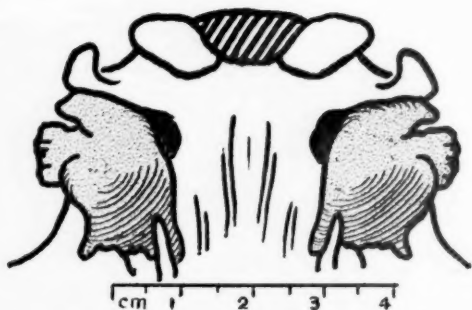
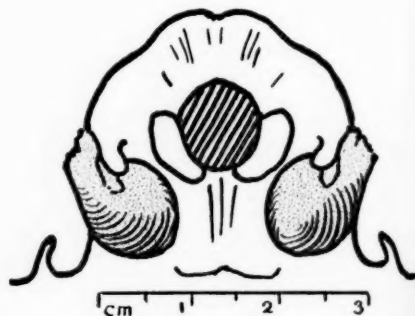
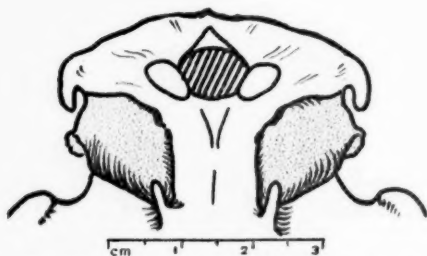
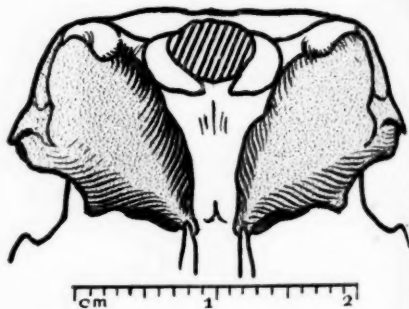
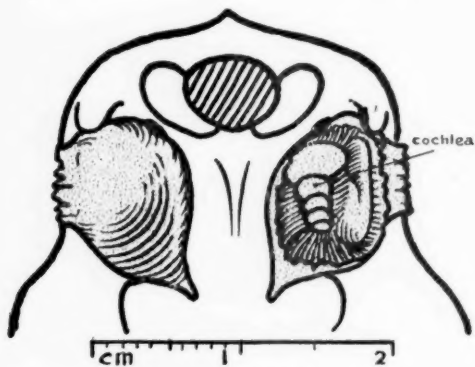
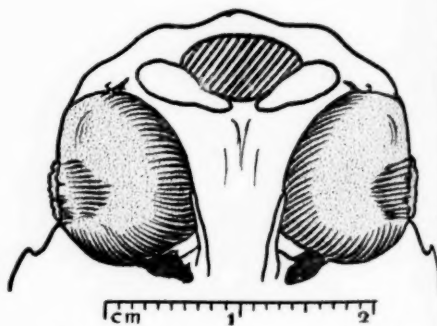
FIG. 27.—*Hystrix africae-australis*: Porcupine.FIG. 28.—*Lepus capensis*: Cape Hare.FIG. 29.—*Thyronomys swinderianus*: Cane Rat.FIG. 30.—*Bathyergus maritimus*: Sand Mole.

FIG. 31.—Guinea-pig.

FIG. 32.—*Geosciurus capensis*: Ground Squirrel.

TYMPANIC BULLA.

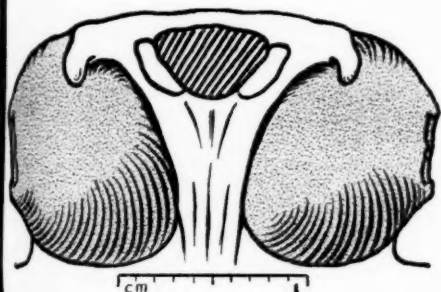


FIG. 33.—*Petromys typicus*: Rock Rat.

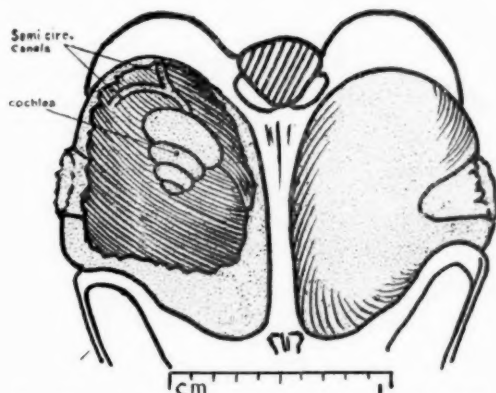


FIG. 34.—*Desmodillus auricularis*: Namaqualand Gerbille.

INSECTIVORES.

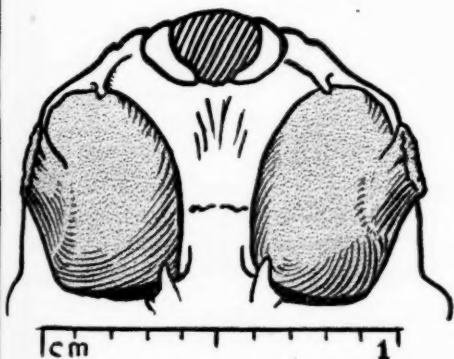


FIG. 35.—*Leggada minutoides*: Field Mouse.

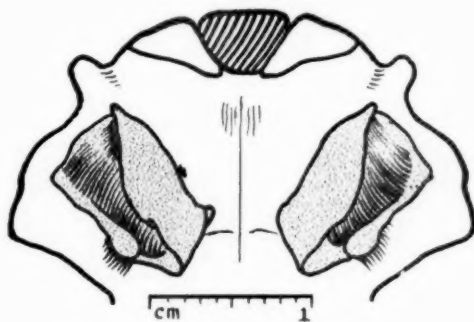
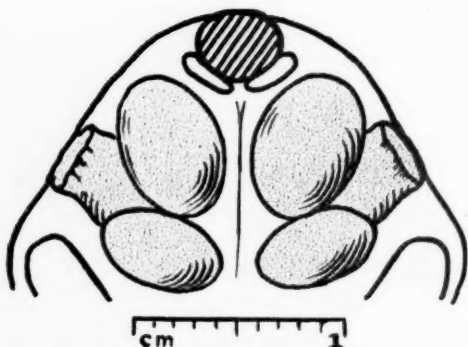
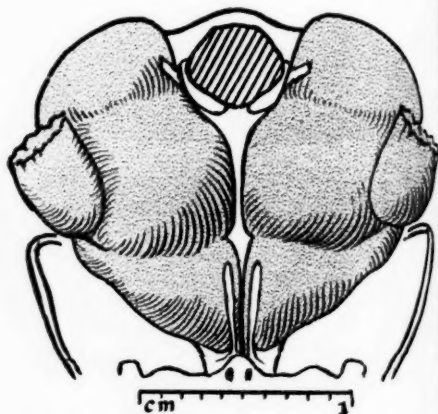
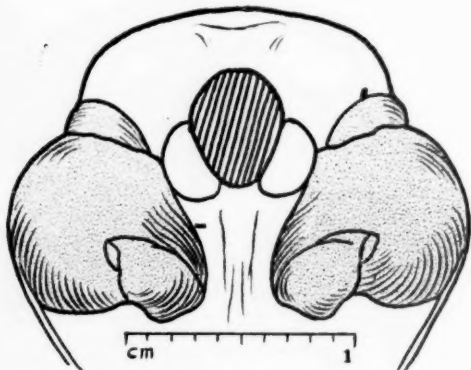
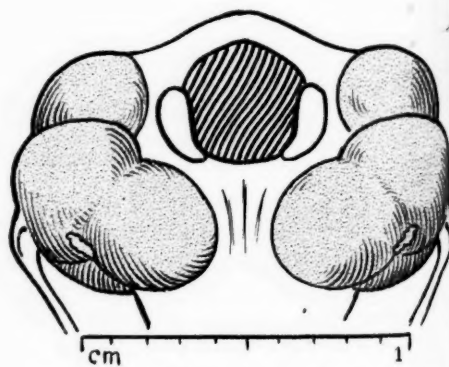


FIG. 36.—*Centetes caudatus*: Tenrec.

FIG. 37.—*Elephantulus rupestris*: Rock Elephant Shrew.FIG. 38.—*Macroscelides probiscideus*: Elephant Shrew.FIG. 39.—*Chrysochloris villosa*: Golden Mole.FIG. 40.—*Chrysochloris namaquensis*: Golden Mole.

TYMPANIC BULLA.

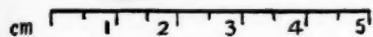
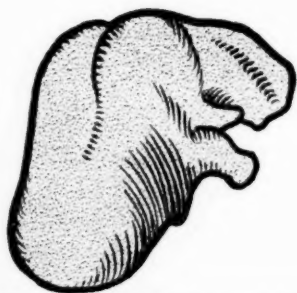


FIG. 41.—Whale: right cetolith, seen from below.

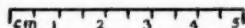
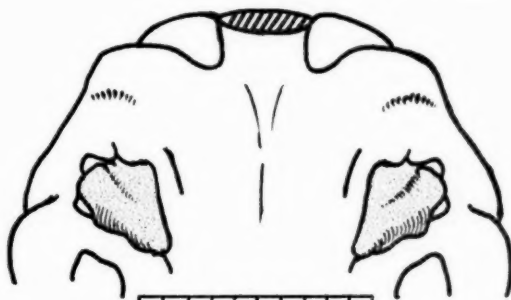


FIG. 42.—*Lagenorhynchus obscurus*: Porpoise.

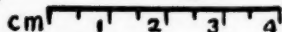


FIG. 43.—*Orycteropus afer*: Aard-vark.

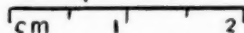
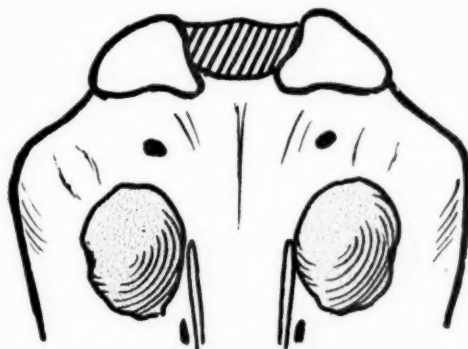


FIG. 44.—*Smutsia temminckii*: Scaly Ant-eater.

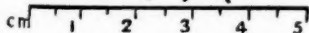


FIG. 45.—Kangaroo.

membranous or cartilaginous, and in the dried skull an open groove is seen (fig. 36). In the Rock Elephant Shrew the anterior part of the os tympanicum, the external auditory meatus, the mastoid part of the os perioticum and probably the alisphenoid are inflated (fig. 37). In another species of Shrew (*Macroscelides probiscideus*), with a slightly smaller skull, the squamosal also shares in the formation of the bulla, and this part is so extensive that the air cavities form bulges which rise a little above the general level of the skull surface. On the base of the skull the

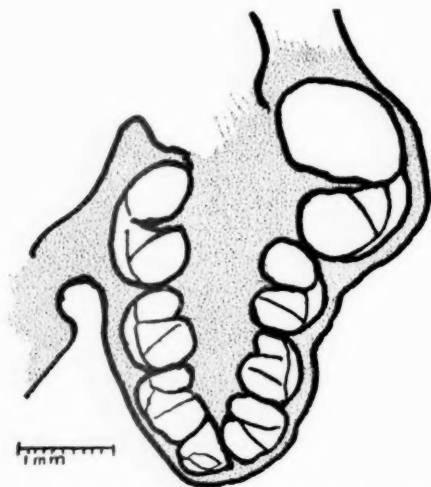


FIG. 46.—Cochlea of the Guinea-pig projecting into the bulla.

Tracing from microphotograph.

front ends of the bullae have inflated the alisphenoid and the basisphenoid. On account of the inflation of the basisphenoid the right and left bullae meet in the median line (fig. 38). Weber (1928) describes the inflation of the basisphenoid by the tympanic bulla as one of the special characteristics of the Insectivores.

The skulls of two species of the genus *Chrysochloris* were selected to show the tympanic bulla condition, the length of skull of *Chrysochloris villosa* being nearly twice that of *Chr. namaquensis* (figs. 39 and 40). *Chrysochloris villosa* has an enormously dilated recessus epitympanicus which extends almost to the top of the skull; this space accommodates the large head of malleus (fig. 74). The recessus epitympanicus becomes part of the bulla and widens the skull on each side; for this reason the dilated

external auditory meatus is relatively short and medially placed (fig. 39). In *Chrysochloris namaquensis* (fig. 40) the epitympanic recess is less dilated, the head of malleus being correspondingly smaller (fig. 75). Owing to the relative shortness of the external meatus the opening of the ear canal comes to lie at the base of the skull in both these species. With the exception of *Chrysochloris* (Golden Mole), where the conditions are completely altered in connection with the dilated epitympanic recess, *Macroscelides proboscideus* (fig. 38) may be taken as an instance of the extreme development of the tympanic bulla. According to Weber (1927) the so-called Wüstentiere show a maximal development of the bulla tympanica. This is linked with their mode of life in the dry air of the desert and with the necessity for sharp hearing. The Shrews and also many small Rodents (*Petromys*, *Desmodillus*) may well be grouped among "Wüstentiere."

Cetaceae.—In the Cetaceae the joined os tympanicum and os perioticum form a rounded mass at the base of skull which is isolated from the surrounding bone, and is joined to the rest of the skull by cartilage and fibrous tissue only. This "tympanic" element often drops away from the skull and is found as a separate bone, called a cetolith on account of its extreme hardness. The right cetolith of the Whale is shown in fig. 41. The os perioticum can easily be separated from the os tympanicum and the ossicles collected from the middle ear cavity. The floor of the os tympanicum is hollowed-out and this part has a peculiar cowrie-shell form. The cetolith of the common porpoise is about one-half the length of the Whale's, but otherwise resembles it very closely (fig. 42).

Other writers have laid stress on the separation of the petrotympanic element from the rest of the skull in the Cetaceae. It implies a certain degree of isolation of the hearing organ in a physiological sense also, because sound vibrations cannot reach the cochlea by conduction through the skull bones. Further, in many species of Whale the external auditory meatus is blocked by a plug of secretion and the tympanic membrane is thick and unable to vibrate (Weber, 1928). Under those conditions sound waves can reach the cochlea only by way of the tympanic bulla.

In the Aardvark (fig. 43) the floor of the tympanic cavity has remained unossified, and in the dried skull the os tympanicum and os perioticum are separate bones. The os tympanicum is present in its primitive form as an incomplete ring with a deficiency above. In the dried skull the tympanic cavity is completely open below. In life the floor of the tympanic cavity is formed partly by membranous tissue and partly by the cartilage of the Eustachian tube (Le Gros Clark, 1926).

In the Marsupials the alisphenoid is said to form the bulla (van Kampen, 1905). This is not the case as regards the Kangaroo. There is no sign of a tympanic bulla, and the bone which apparently separates the meatal

part of the os tympanicum from the os perioticum is a large paroccipital process belonging to the exoccipital skull element (fig. 45).

THE AUDITORY OSSICLES (figs. 47-77).

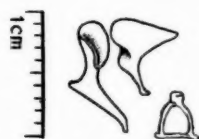
It is not easy to obtain a representative collection of auditory ossicles from prepared animal skulls. In the completely dried specimens, where all the cartilage and fibrous tissue have been destroyed by *Anthrenus* beetle larvae, the ossicles have become loose and tend to get lost during the handling and transport of the skulls. When the meatus is large and shallow the ossicles drop out through that opening. But they may also get lost through the floor of the bulla, if this has remained unossified, or through a specially short and wide Eustachian tube. In very small Mammals (e.g. Bats, Shrews, Mice) the ossicles are such minute structures that it is difficult to find them. However carefully one breaks away the floor of the bulla and the walls of the epitympanic recess, the ossicles, if they have not dropped out before, get detached and often become lost among the chips of bone resulting from the dissection. Necessarily therefore our collection of these is somewhat limited.

The *malleus* has a rounded head in Primates, Ungulates, Carnivores and Rodents. In some of the Insectivores (fig. 73) and Marsupials (fig. 77) the head has a flat, lamellar shape. If, in addition to the flat shape, the anterior process is well developed, the malleus assumes a sickle or horse-shoe shape (fig. 77). The significance of the great enlargement of the malleus head in many species of *Chrysochloris* is quite obscure. For instance, in *Chrysochloris villosa* (fig. 74) the malleus head is actually nearly three times as thick as that of man (fig. 47), although the total skull length of the animal is only 3 cm. The slender handle of the malleus in the specimen represented in fig. 74 was broken off, but the character of the handle of the malleus can be seen in fig. 75, which shows the malleus and incus of a different species of *Chrysochloris*. In many of the Carnivores and in some Ungulates the anterior process of the malleus is joined to the head by a flat piece of bone (figs. 53, 57, 60, 62 and 63). This may represent a transition form between the round-headed malleus and the primitive lamellar shape.

The *incus*, apart from differences in actual size, is much less variable in shape throughout the mammals. The *incudo-malleolar joint* is not always the freely movable articulation that the Helmholtz theory postulates. In man the union between malleus and incus must be described as a pseudo-symphysis with an irregular fibro-cartilage interposed (Keen, 1930). In many mammals there is a definite synostosis, and in that case the joint

AUDITORY OSSICLES.

PRIMATES AND LEMURS.



47.—Man.



FIG. 48.
Baboon.



FIG. 49.
Macaque.



FIG. 50.
Garnett's Lemur.



FIG. 51.
Moholi Lemur.

UNGULATES.

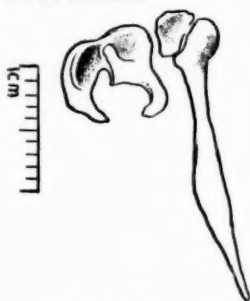


FIG. 52.—Elephant.



FIG. 53.
Giraffe: Malleus head
broken off.



FIG. 54.
Buffalo.



FIG. 55.
Horse.

CARNIVORES.



FIG. 56.—Zebra.



FIG. 57.
Springbuck.



FIG. 58.
Steenbok.

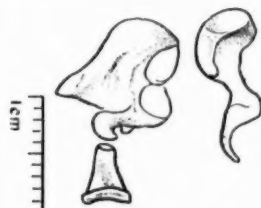


FIG. 59.—Sea Leopard.



FIG. 60.—Tiger.



FIG. 61.—Hyæna.



FIG. 62.—Hunting Dog.



FIG. 63.—Cat.

RODENTS.



FIG. 64.—Genet:
Malleus head broken off,
and fused with incus.



FIG. 65.
Skunk.



FIG. 66.
Porcupine.



FIG. 67.
Cape Hare.



FIG. 68.
Rabbit.



FIG. 69.
Guinea-pig.



FIG. 70.
Rock Rat.



FIG. 71.
Mouse.



FIG. 72.
Gerbille.

INSECTIVORES.



FIG. 73.—Ossicles from three
different types of Shrew.



FIG. 74.—Golden Mole
(*Chrys. villosa*).



FIG. 75.
Golden Mole
(*Chrys. managuensis*).



FIG. 76.—Whale.



FIG. 77.—Kangaroo.

is obviously quite immovable; *e.g.* in some small Carnivores (fig. 64) and in many Rodents (figs. 66, 67, 68, 69, 70, and 72).

The *stapes* is generally lost in the dried skulls, and for this reason only a few appear in the sketches. It is usually shaped like the human stapes with two limbs, but it may be a solid plate. The latter shape is found in the large mammals living in the sea (figs. 59 and 76). The stapes of the Whale shows in addition a synostosis with the margins of the fenestra ovalis; the little bone has to be broken away from the oval window. The malleus was free, although in some species of Whale the hammer bone is stated to show bony union with the walls of the tympanic cavity (Weber, 1928). The ossicles in the Whale are obviously not used for sound conduction according to the Helmholtz theory.

DISCUSSION.

The Helmholtz Theory of Sound Conduction.—Helmholtz formulated his classical theory with the anatomical condition of the human ossicle chain in mind (1896). The vibrations of the tympanic membrane carry the handle of malleus with it. The head of malleus moves in an opposite direction, because it lies above an "axis of rotation" which is represented by a line drawn from the tip of the short process of incus, across the lower part of the head of malleus to the anterior process of malleus; the latter process is only a spicule on the human malleus prolonged by a fine ligament (fig. 78). The Helmholtz theory further postulates a "locking" mechanism



FIG. 78.—Auditory ossicles of Man; articulated.
Line *a-b* shows the axis of rotation.

in the incudo-malleolar joint formed by a small projection on the lower margin of the articular area of the head of malleus, fitting a corresponding spur on the incus. When the tympanic membrane moves inwards the head of malleus, lying above the axis of rotation, moves outwards; the incudo-malleolar joint "locks" and the incus follows the head of malleus. The resulting movement of the long process of the incus, which projects below the axis of rotation, and therefore the movement of the stapes also, is in the same direction as that of the tympanic membrane. If, however, the tympanic membrane moves outwards from its resting position, as might result from a fall of air pressure outside the tympanic membrane, the incudo-malleolar joint "unlocks" and the incus fails to follow the movement of the malleus.

The long process of the incus projects a shorter distance below the axis of rotation than the handle of the malleus. For that reason the vibratory movements of the tympanic membrane are converted into movements of a smaller amplitude before they reach the oval window. The vibrations of the tympanic membrane are transmitted as a whole and the fenestra ovalis is stated to be the only channel by which sound waves reach the fluids of the cochlear canals.

There are many objections to Helmholtz's explanation of sound conduction across the middle ear cavity. For instance, it is impossible to maintain that the incudo-malleolar joint is a freely movable articulation. Microscopic sections of the joint usually show an irregular fibro-cartilage (Keen, 1930), and one should describe the joint as a form of synchondrosis with very little independent movement between the bones. The "locking" mechanism operates only with inward movements of the tympanic membrane, while the "unlocking" or protective mechanism comes into play with outward movements. But a compression of the tympanic membrane due to a sudden wave of increased pressure in the meatus is a greater danger to the cochlea, and yet there is no protective mechanism against this inward movement.

When we approach the problem of sound conduction from the standpoint of comparative anatomy, all the evidence is against the classical Helmholtz theory. A satisfactory theory of sound conduction should take into account the condition of the auditory ossicles in the whole mammalian family. The cochleae are very similar in the mammals, and this to a large extent irrespective of the size of the animals (Keen, 1939); we may assume that the physiology of sound reception is the same process in all. But as regards sound conduction we are faced with an extraordinary diversity of anatomical conditions which are quite impossible to fit into the scheme of a delicately adjusted system of levers vibrating in sympathy with the tympanic membrane. The arguments against the Helmholtz theory based on comparative anatomy may be summarised as follows:—

(a) The auditory ossicles are so variable that it seems difficult to accept that they are mechanically adapted to conduct sound in the manner described by Helmholtz. The minute ossicles found in Rodents and Insectivores are clearly useless for a complicated sound conduction process, and may be looked upon as vestigial structures. The extraordinary condition of the malleus in some species of *Chrysochloris* has been studied previously (Forster Cooper, 1928). The top-heavy spherical head of the malleus has a small incus adhering to it below the level of the axis of rotation; this would make any vibration in the Helmholtz sense quite impossible. There is no reason to think that these mole-like animals are deaf. On the contrary, we may assume that their hearing, like that of

other Moles, is exceedingly acute. According to Brehms (1912), Moles (*Talpa*), tightly enclosed in their narrow runs, hear the slightest sound which is transmitted through the earth to the whole body surface.

(b) Bony union often exists between the ossicles, *e.g.* many Rodents, some small Carnivores, Whale.

(c) There is no regular size relation between the tympanic ring, *i.e.* the diameter of the tympanic membrane, and the malleus. To give a few instances, actual measurements are:

Homo sapiens: diameter of tympanic membrane 8–10 mm., length of malleus 9 mm.

Guinea-pig: diameter of tympanic membrane 6 mm., joined head of malleus and incus 3.5 mm.

Shrew: diameter of tympanic membrane 5 mm., length of malleus 3 mm.

Chrysochloris: diameter of tympanic membrane 3.5 mm., head of malleus across 8 mm.

There have always been a small group of physiologists and otologists who have taken the view that the tympanic membrane and ossicles have little or no importance in the conduction of sound to the cochlea (Zimmermann, 1903 and 1904; Zünd-Burguet, 1914). An acceptable theory must also account for the fact that the removal of the drum membrane and ossicles in operations for chronic middle ear suppuration does not necessarily cause severe deafness. Many cases are on record of fairly good hearing despite the absence of these structures (Keen, 1926). Therefore sound vibrations are able to reach the cochlea by methods other than the vibrations of the ossicular chain. It may be sound conduction through solid bone or directly across the air of the tympanic cavity on to the promontory, which is the part of the cochlea least covered by bone. In mammals with small and presumably vestigial ossicles these alternative routes assume correspondingly greater importance.

The Tympanic Bulla as a Physiological Hearing Adaptation.—We may compare the cochlea to a delicate microphone placed deeply in the region of the base of the skull. The fluids in the cochlear canals will pick up sound vibrations which reach it by any of the various available routes. It is quite unknown which is the most important route. But we incline to the view that sound transmission across the air of the tympanic cavity or bulla direct on to the bony wall of the cochlea is much more important than sound conduction *via* the ossicles and fenestra ovalis. This view is the only one which can be reconciled with the great variability of the ossicles and their apparently vestigial character in small mammals.

As the tympanic bulla grows and extends, it hollows out the cochlea from the petrous bone, until in extreme cases the inner ear forms a knob

projecting into the air cavity. A cochlea of this type may have a shell-like covering so thin that the turns of the cochlea can be counted with the naked eye. Such a mechanism is undoubtedly a better physical instrument for picking up sound vibrations from the air inside the bulla than would be a cochlea surrounded by a thick wall of bone. If one considers the significance of the bulla in this light, one is also offered an explanation why the bulla is placed at the *base* of the skull beneath the *front part* of the os perioticum. This anatomical position is most likely connected with the position of the cochlea, which first appeared as an outgrowth of the *anterior and lower part* of the membranous labyrinth.

The tympanic bulla is said to be a late development ontogenetically (van Kampen, 1905). That observation is in accord with our conception of the bulla as an adaptation for the better transmission of air-conducted sounds. In spite of the great forward step in evolution represented by the development of the mammalian ossicles from the jaw bones of the Reptiles, it would appear that these ossicles were not of themselves adequate to solve all the demands in respect of sound conduction. We suggest that in many mammals, but especially in the small species, the ossicular chain assumed a vestigial character, and that in them an additional step in the evolution of the sense of hearing was taken, viz. the formation of a tympanic bulla.

We are greatly indebted to Dr. E. L. Gill, Director of the South African Museum, Cape Town, for his kindness in giving us free access to his collection of mammalian skulls.

SUMMARY.

The authors have made a comparative survey of the tympanic bulla in mammalian skulls. This is illustrated by drawings of the posterior part of the base of skull of 45 different species, including types representing all the main mammalian orders, and ranging from the large to the very small animals. The study establishes as a broad principle that the tympanic bulla is a feature of small animals and tends to be absent in the larger ones.

In the second part of the article the auditory ossicles are described and discussed from the same standpoint. The ossicles show great variations from species to species, and in some mammals very extraordinary conditions are found (*e.g.* the relatively gigantic malleus in the Golden Mole). Then follows a brief discussion of the Helmholtz theory of sound conduction as applied to the human auditory ossicles. The authors maintain, in opposition to the orthodox view, that the ossicles in most small mammals are not adapted mechanically to conduct sound in the

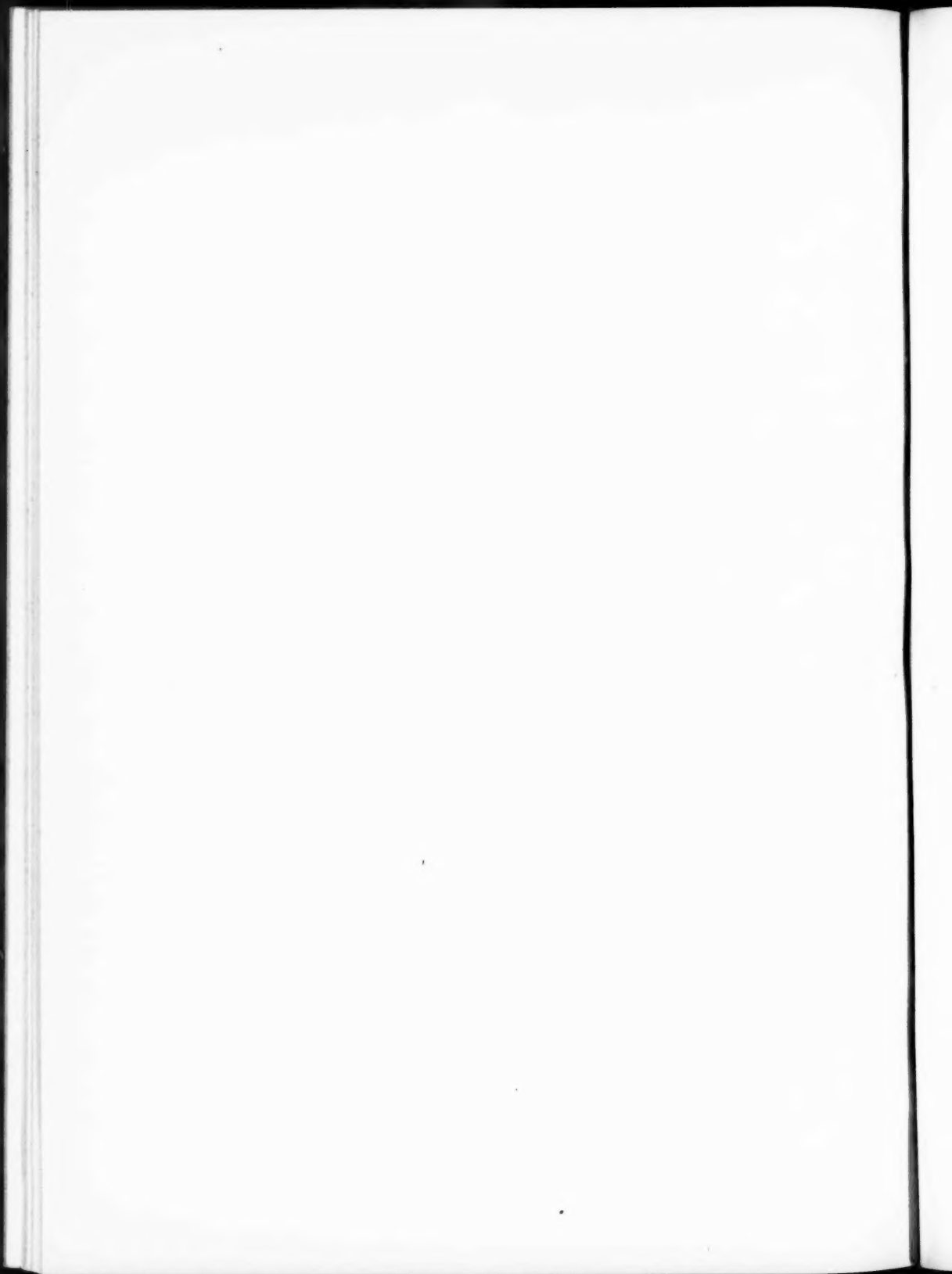
manner postulated by Helmholtz. It is suggested that the small, irregularly shaped and often ankylosed ossicles of many mammals are merely vestigial structures; and further, that sound waves reach the cochlea direct through the air of the tympanic cavity rather than *via* the ossicular chain and the fenestra ovalis.

Lastly, the view is advanced that the tympanic bulla is a hearing adaptation, because the bony covering of the cochlea is thinned-out when the bulla is extensive. There are several illustrations in the text which show the cochlea actually projecting into the air cavity of the tympanic bulla, with a bony covering which is so thin that the turns of the cochlea can be counted with the naked eye. Such a cochlea is obviously a better physical instrument for picking up air-borne sound vibrations than a cochlea covered by a thick shell of bone.

The Council desires to acknowledge the receipt of a grant from the University of Cape Town towards the cost of publication of this paper.

REFERENCES.

- FORSTER COOPER, C. (1928). "On the ear region of certain of the Chrysocloridae," Trans. Roy. Soc. London.
- LE GROS CLARK, W. E., and SONNTAG, C. F. (1926). "A monograph of *Orycteropus afer*," P.Z.S., p. 447.
- LE GROS CLARK, W. E. (1934). *Early Forerunners of Man*. London, Ballière, Tindall & Cox.
- HELMHOLTZ (1896). *Die Lehre von den Tonempfindungen*.
- VAN KAMPEN, P. N. (1905). "Die Tympanalgegend des Säugetierschädels," *Morphologisches Jahrbuch*, Bd. 34, S. 321.
- KEEN, J. A. (1926). "An investigation of the end-results of sixty cases of radical mastoid operation with special reference to hearing," *Journ. Laryngol. and Otol.*, March.
- KEEN, J. A. (1930). "Ankylosis of the malleus and incus," *Journ. Laryngol. and Otol.*, December.
- KEEN, J. A. (1939). *J. Anat. Lond.*, vol. lxxiii, p. 592.
- VAN DER KLAUW, C. J. (1931). "The auditory bulla in some Fossil Mammals," *Bull. of American Museum of Natural History*, vol. lxii.
- "Brehms Tierleben" (1912). *Säugetiere*, Bd. I, S. 313. Leipzig und Wien, Bibliographisches Institut.
- WEBER, MAX (1927-28). *Die Säugetiere*, Bd. I, pp. 70, 75, 202; Bd. II, pp. 98, 375. Jena, Gustav Fischer.
- WINTERSTEIN, H. (1913). *Handbuch der vergleichenden Physiologie*, Bd. IV, S. 928.
- ZIMMERMANN (1903). "Arbeiten der letzten Jahre über die Physiologie der Schalleitung im Ohre," *Internat. Zentralblatt. f. Ohrenhkl.*, Bd. I, Heft 3, S. 105.
- ZIMMERMANN (1904). "Der physiologische Wert der Labyrinthfenster," *Arch. f. Anat. und Physiol.*, suppl. Bd., S. 193.
- ZÜND-BERGUE, A. (1914). *Conduction Sonore*. Paris, A. Maloine.



THE LIFE-HISTORY OF *CYCLOGRAPSPUS PUNCTATUS*,
M. EDW.: BREEDING AND GROWTH.

By G. J. BROEKHUYSEN, Ph.D., F.A.G.S., Department of Zoology,
University of Cape Town.

(With Plates LVI, LVII, and eleven Text-figures.)

(Read April 17, 1940.)

CONTENTS.

	PAGE		PAGE
INTRODUCTION	331	DISCUSSION	362
BREEDING	333	SUMMARY	364
GROWTH	348	ACKNOWLEDGMENTS	365
SEX-RATIO	362	LITERATURE	365

INTRODUCTION.

Cyclograpsus punctatus (Pl. LVI, figs. 2, 3) is a crab which is more or less common along the greater part of the South African coast (Stebbing, 1910; Stephenson, Stephenson, and du Toit, 1937; Stephenson, Stephenson, and Bright, 1938; Bright, 1938; Eyre, Broekhuysen, and Crichton, 1938; unpublished information obtained by Stephenson and his co-workers). This species is not confined to South African shores, but according to Rathbun (1918) has also been recorded from South America (Chile) and China, while *C. caudouinii*, M. Edw., which several authors consider to be the same species or closely related to it, has been found in New Guinea, Australia, and New Zealand. Balss (1922) describes *C. punctatus* as a circum-subantarctic species.

In South Africa this species inhabits the higher parts of the intertidal zone (Pl. LVI, fig. 1). It seems to prefer those parts of the shore which are very much broken up and which enable it to find shelter under and among the boulders as well as in the crevices. The species can apparently stand great variations in salinity as it also frequents river-estuaries. It was found by the author to occur in the upper part of the mouth of the Buffalo River at East London and at the upper end of the land-locked Knysna River estuary.

As the species was particularly abundant at Strandfontein and at St. James, both on the False Bay coast (text-fig. 1), there was an opportunity

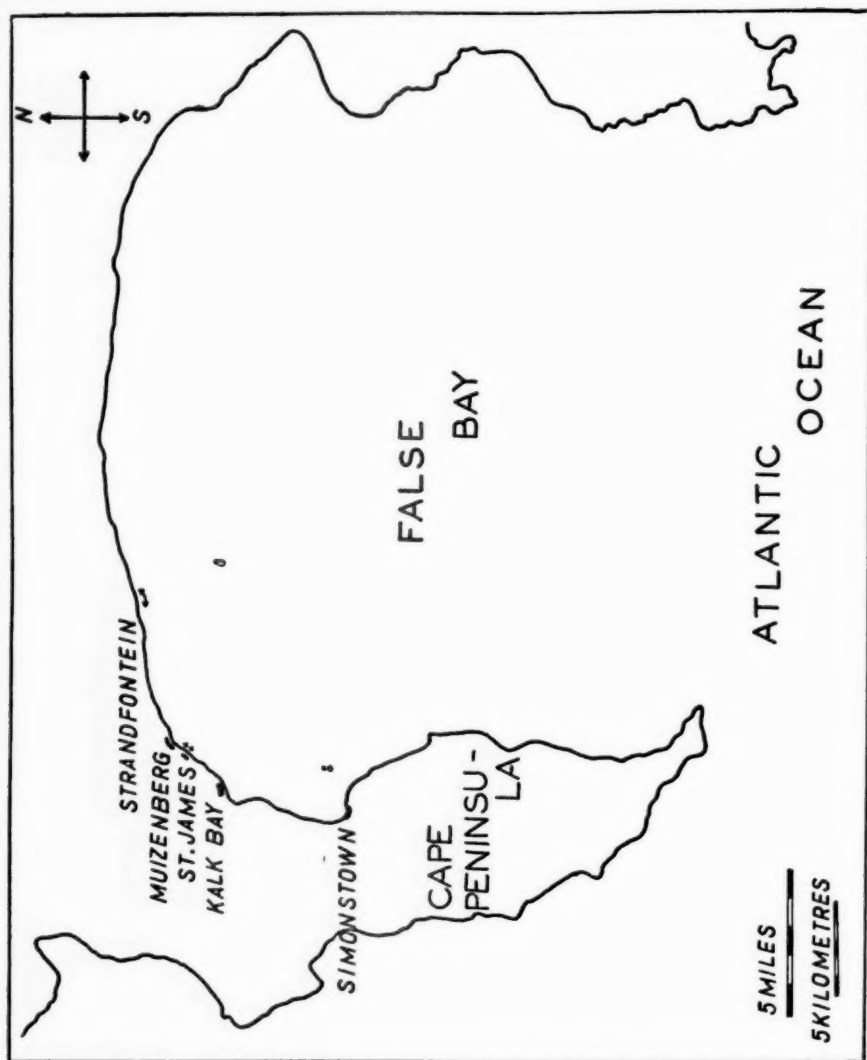


FIG. 1.—A map of False Bay, showing the places at which material was collected. (Based on part of Admiralty Chart No. 2082, 1914 edition.)

of studying its life-history. The objects of this study were (a) to increase our knowledge of the life-histories of the South African marine Crustacea, which [except for the crawfish *Jasus lalandii* (M. Edw.) Ortmann, whose life-history has been studied by Gilchrist (1916, 1918, and 1920), von Bonde and Marchand (1935), von Bonde (1936)] still forms a practically untouched field for research, and (b) to compare the life-history of this crab, living in a southern temperate region, with that of *Carcinides* (*Carcinus*) *maenas* (L.), a common littoral and sublittoral Brachyuran species from the shores of northern temperate regions, which has recently been the subject of an investigation by the present author (Broekhuysen, 1936).

This paper deals with breeding and growth only, and the material used was collected almost exclusively at Strandfontein. Only in a few cases has material from St. James been included. Some data were obtained from material collected at East London, in order to see whether there was any indication of a difference in breeding-season between these and the Strandfontein crabs.

BREEDING.

Introduction.—In order to find out whether the gonads in the species under consideration showed any periodicity in their activity, as many crabs as possible were collected, twice a month, for a period of one and a half years (May 1937–October 1938). During the last half of June and the whole of July 1937, however, no crabs could be collected owing to the author's absence. The crabs were collected at random, except during the period May to 12th October 1938, when only berried females were collected. Except for this last period, therefore, the material collected consisted of crabs of both sexes and of all sizes. As soon as the material had been brought to the laboratory the males and females were sorted out and measured, the greatest width of the carapace being taken as the index of size. The egg-bearing females were separated from the rest of the females and the developmental stage of the eggs was determined. After this had been done all crabs with a carapace-width greater than 8.8 mm. were dissected, and the developmental stage of their gonads determined. The dissection was done by making a transverse incision at the posterior margin of the carapace where the latter touches the first abdominal segment, after which the carapace could be lifted up and the gonads exposed.

Gonad-activity of the Males.—Altogether 1786 males caught at Strandfontein were dissected, and the developmental stage of their gonads recorded. According to the appearance of the paired genital tubes it was possible to distinguish three stages of development, namely: I, Gonads developed very little or not at all; II, Gonads developing; and III, Gonads well developed. It was not always easy to distinguish whether a particular

crab's gonads were in Stage I or Stage II, but on the whole this could be determined. The results of the dissections are summarised in Table I and are expressed graphically in text-fig. 2.

TABLE I.

Developmental Stages of the Gonads of Males from Strandfontein during the period 2/5/37 to 30/4/38.

Date.	Number of males more than 8.8 mm. across carapace.	Undeveloped gonads (Stage I).		Developing gonads (Stage II).		Well-developed gonads (Stage III).	
		Num-ber.	Per-centage.	Num-ber.	Per-centage.	Num-ber.	Per-centage.
2/5/37	62	21	33.9	25	40.3	15	24.2
18/5/37	77	30	39.0	29	37.7	18	23.4
5/6/37	69	30	43.5	24	34.8	15	21.7
10/8/37	50	33	66.0	8	16.0	8	18.0
24/8/37	91	62	68.1	22	24.2	7	7.7
29/9/37	107	63	58.9	31	29.0	13	12.1
15/10/37	110	56	50.9	43	39.1	11	10.0
25/10/37	100	54	54.0	32	32.0	14	14.0
10/11/37	125	46	36.8	68	54.4	11	8.8
29/11/37	93	35	37.6	37	39.8	21	22.6
13/12/37	78	14	17.9	21	26.9	43	55.1
30/12/37	88	33	37.5	24	27.3	31	35.2
14/1/38	97	45	46.4	30	30.9	22	22.7
31/1/38	76	31	40.8	23	30.3	22	28.9
10/2/38	105	22	21.0	24	22.9	59	56.2
24/2/38	99	16	16.2	22	22.2	61	61.6
12/3/38	111	28	25.2	20	18.0	63	56.8
30/3/38	68	5	7.4	14	20.6	49	72.1
12/4/38	84	5	6.0	18	21.4	61	72.6
29/4/38	96	3	3.1	11	11.5	82	86.1

Table I and text-fig. 2 reveal the existence of a distinct periodicity in the activity of the male reproductive organs. The chief breeding-season falls in the late summer and autumn months (February to May). There seems, however, also to be a distinct, though restricted, increase in the number of males with ripe gonads in the months November and December, with a maximum in the latter. This increase is followed by a temporary decrease in activity in January, after which the principal breeding-season starts. The fact that this small maximum is preceded by an increase in

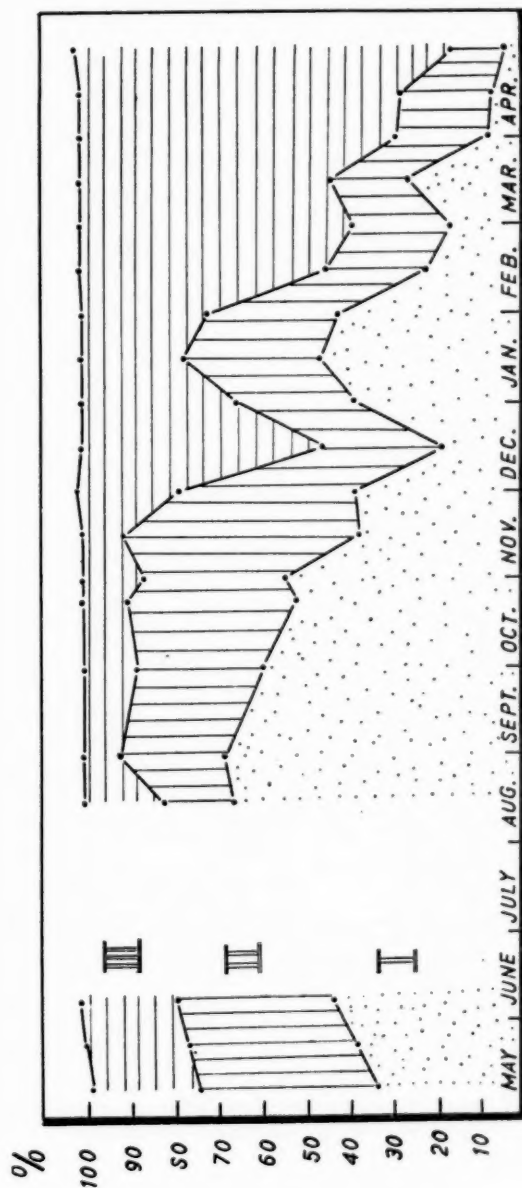


FIG. 2.—The developmental stages of the male gonads in *C. punctatus* during the period May 1937 to April 1938. Three different stages of development are distinguished (see text, p. 333). The width of each shaded area represents the percentage of males which had their gonads in that particular stage.

the number of individuals with their gonads in the developing stage (see text-fig. 2) suggests that this irregularity in the curve indicates the existence of a real, though subsidiary, additional breeding-season (see also p. 339). The males of *C. punctatus*, therefore, appear to have two more or less distinct breeding-seasons.

During the winter and spring the gonads of the majority of them enter a resting period, but even at the height of this season, in September to October, about 10 per cent. of the males have ripe gonads, the genital tubes in these animals being much swollen.

Gonad-activity of the Females.—Altogether 3438 females with a carapace-width exceeding 8.8 mm. were examined, and the number of berried females among them recorded. 2596 females without extruded eggs were dissected, in order to follow the development of their gonads over a period of a whole year. Practically all the crabs came from Strandfontein, and only on one occasion (17/9/37) were crabs from St. James included. Among these females four different developmental stages were distinguished, namely: I, Ovaries developed very little or not at all; II, Ovaries developing; III, Ovaries strongly developed; IV, Eggs extruded. The developing and strongly developed ovaries had a dark purplish appearance due to the yolk of the eggs.

The results are summarised in Table II and in text-fig. 3. Text-fig. 3 consists of two parts. The curves in the upper part represent percentages of females more than 8.8 mm. across the carapace, with extruded eggs, during the period May 1937 to October 1938. The lower part of the figure gives the percentages of females with gonads in the four different stages distinguished, during the period May 1937 to May 1938.

Table II and text-fig. 3 indicate a definite periodicity in the gonad-activity of the females, the chief breeding-season coinciding with the winter months (May to September), while a minor breeding-season occurs in January and February. These conclusions are further supported by other facts discussed below (see Table IV, p. 342). The periods October to January and February to May are the periods during which the majority of the females appear to be sexually inactive. Just as in the males, there is no season at which gonad-activity is completely suspended, for even at the time when this activity is at its minimum some females can be found with well-developed ovaries or even extruded eggs. Of the females kept *in captivity* during the course of this investigation eighteen extruded eggs. The months in which this occurred and the number of spawning individuals were as follows: June, 6; July, 3; August, 4; September, 1; October, 1; December, 1; January, 2. These data obtained from individuals under laboratory conditions correspond rather well with those referring to crabs in their natural habitat.

The Activity of the Reproductive Organs in the Female Crabs during the several Months of the Year.

[illegible]

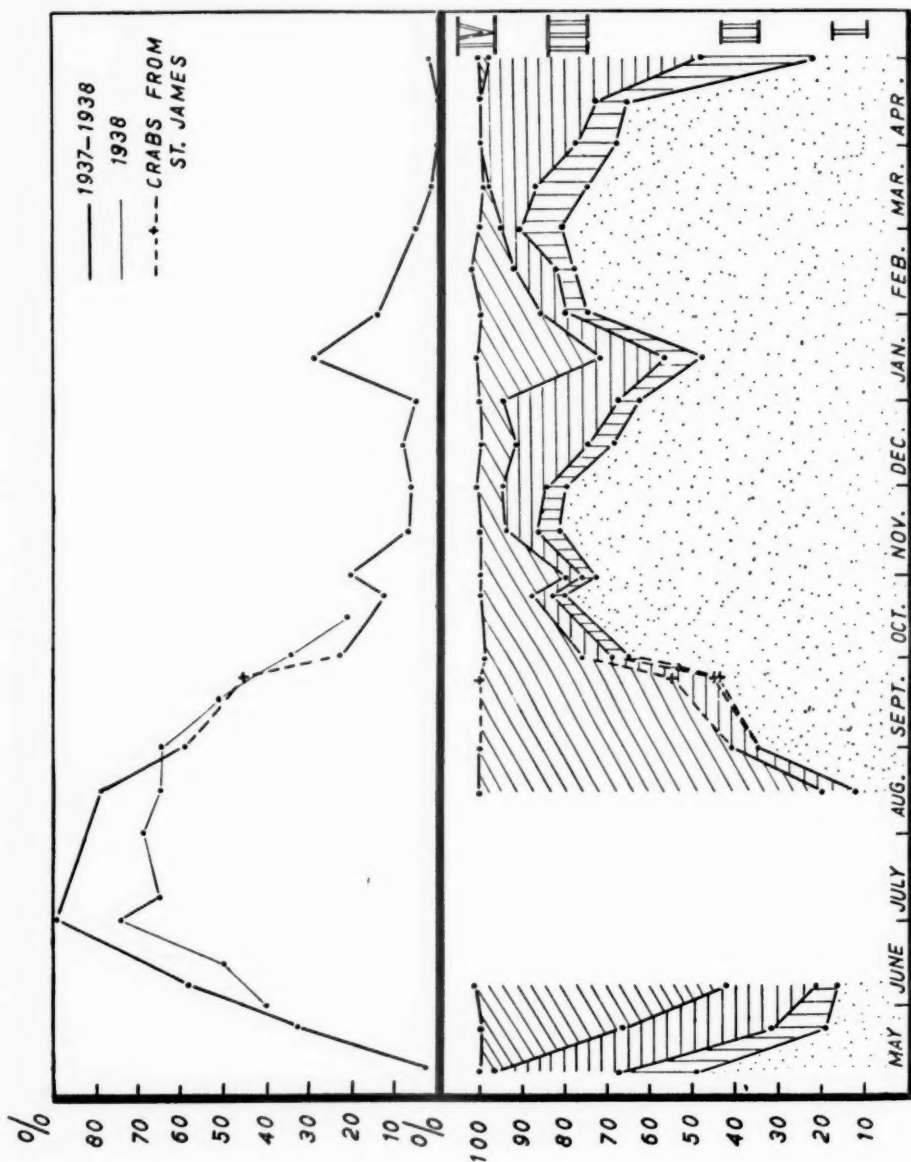


FIG. 3.—A. The percentage of berried females. B. The developmental stages of the female gonads in *C. punctatus* during the period May 1937 to April 1938. Four different stages in development are distinguished in the text (p. 326). The width of each shaded area represents the percentage of females which have their gonads in that particular stage. The berried females are again included here.

The Relationship between the Gonad-activity of the Males and that of the Females.—If text-figs. 1 and 2 are compared, the following facts will become clear. During the main breeding-season of the females, which falls chiefly in the winter and early spring, the majority of males appear to have gonads in a resting stage. This might be expected because during this period copulation cannot take place, owing to the fact that the majority of females have eggs under the abdomen. This principal breeding-season of the females is preceded by a period of maximal gonad-activity in the males in February, March, and April, which suggests that copulation probably takes place one or more months before the females extrude their eggs.* The minor breeding-season of the females, which has its maximum in January, is also preceded by an increase of gonad-activity in the males, which shows a maximum in December. It is therefore likely that these females copulated in December. Evidently the reproductive rhythm of the one sex is suitably adjusted to that of the other.†

The Number of Egg-batches extruded by each Female during a Single Breeding Period.—After it had been found that the females had two breeding periods in the course of the year the question arose as to whether a single female extruded one or more batches of eggs during a breeding-season. Dissections of females in berry (see Table III) revealed that, although the majority had their gonads more or less at rest, a fair number appeared to have developing or nearly ripe gonads. This suggested the probability that a female might extrude more than one batch of eggs in a single breeding-season.

The number of crabs in berry dissected is very small for the months November to March owing to the rapid decrease in the number of these crabs towards the end of the breeding-season. The percentages for those months are therefore very inaccurate.

To elucidate this point it was necessary to study the stages of development of the eggs carried by the berried females in the breeding-season. In the development of the egg of *C. punctatus*, and indeed of the *Brachyura*

* It is remarkable that during the whole period of the investigation only two cases of copulation between female and male were noticed. In addition, on one occasion a male was observed to attempt copulation with another male. It is therefore likely that copulation takes place during the night and that it only lasts for a short time. The copulations actually observed occurred in the months April and May and both partners were in a hard condition.

† On the 15th and 17th of July 1937 the author collected 106 individuals of *C. punctatus* at the mouth of the Buffalo River at East London. Of the 66 females with a carapace-width exceeding 8.8 mm., 47 (71 per cent.) had extruded eggs. This high percentage suggests that at this latitude also the height of the breeding season falls in July.

TABLE III.

The Developmental Stage of the Gonads of Females in Berry.

Date.	Developmental stage of ovary.					
	Young.		Developing.		Strongly developed.	
	Number.	Percentage.	Number.	Percentage.	Number.	Percentage.
15-18/7/37 *	17	37.0	9	19.6	20	43.5
10/8/37	56	75.7	7	9.5	11	14.9
24/8/37	31	81.6	5	13.2	2	5.3
29/9/37	18	81.8	1	4.5	3	13.6
25/10/37	25	92.6	1	3.7	1	3.7
10/11/37	11	100.0	0	0.0	0	0.0
29/11/37	8	88.9	0	0.0	1	11.1
13/12/37	9	90.0	1	10.0	0	0.0
30/12/37	3	60.0	1	20.0	1	20.0
14/1/38	31	70.5	5	11.4	8	18.1
31/1/38	14	87.5	0	0.0	2	12.6
24/2/38	6	85.7	1	14.3	0	0.0
12/3/38	0	0.0	3	100.0	0	0.0

* These crabs were caught at the mouth of the Buffalo River at East London. The rest of the crabs were caught in False Bay.

in general, the following twelve stages can be distinguished by examining the living eggs microscopically:—

Stage I. No segmentation has yet occurred and no external cleavage is visible.

Stage II. The first cleavages have taken place (Pl. LVII, fig. 1).

Stage III. A considerable number of cells have been formed.

Stage IV. Cells very numerous.

Stage V. For the first time a yolk-free (transparent) part begins to show itself. This stage coincides with the appearance of endoderm cells and of a slight invagination (Korschelt and Heider, 1909, 1910, and Balss, 1927) (Pl. LVII, fig. 2).

Stage VI. A more or less distinct division into a yolk-free and a yolk-containing part is now clearly visible. This stage comprises the whole period between the first indication of the formation of germ-layers and the appearance of the eye-pigment of the larvae (Pl. LVII, fig. 3).

Stage VII. The first sign of eye-pigment is visible.

Stage VIII. Pigment-bands have been formed.

Stage IX. The larvae are strongly pigmented, the amount of yolk remaining is still fairly large.

Stage X. The yolk has been reduced to two small separate patches (Pl. LVII, fig. 4).

Stage XI. The prezoa larvae are escaping from the egg-capsules (Pl. LVII, fig. 5).

Stage XII. Only empty egg-capsules and eggs containing dead larvae are left, and the batch of young can be considered as having hatched.

The prezoa (protozoa), as a free living stage, lasts only for a very short time in this species, since moulting takes place almost immediately after the larva has hatched. Most of the prezoae have in fact already attained the first zoea stage (Pl. LVII, fig. 6) before escaping from beneath the crab's abdomen.

During the period May 1937 to May 1938 a total number of 533 egg-batches was examined and the stage reached by the eggs in each batch was recorded (Table IV). No observations were obtained for the last half of June and the whole of July 1937, on account of the author's absence.

As this period appeared to coincide with the height of the winter breeding-season, Table IV provides no information as to the number of egg-batches produced by any one female during this major season. For this reason a further total of 463 egg-batches was studied during the period 27/5/38 to 11/10/38, and the results of this examination are graphically expressed in text-fig. 4. This figure reveals the following facts:—

(a) The variation in the developmental stages of the eggs of different batches is considerable, a point which is also brought out by Table IV.

(b) In spite of this considerable variation, there is a suggestion that three different lots of fresh egg-batches were produced during the winter breeding-season of 1938. The first lot of eggs appeared in the second and third week of May, and most of these hatched during the first and second week of July. In the second week of July the majority of the crabs examined extruded a fresh batch of eggs, and these hatched during the second and third week of September. In the second week of September a third lot of fresh egg-batches appeared. In October, which is at the end of the winter breeding-season, eggs in various different developmental stages occur and no maximum can be made out. Text-fig. 4 further suggests, that the second and third of these three extrusions of eggs may have been made by the same females as those which made the first extrusion, or that at least this may have happened in a proportion of cases. The only other possibility is that, if a given female extrudes eggs once only during the season, the females tend to ripen in successive groups, with rather distinct gaps between the ripenings. From the information before us this possibility seems less likely than the first. If it is true that

TABLE IV.

*Stages of Development of the Eggs carried by the Berried Females during the period May 1937 to May 1938. Almost all the Crabs came from Strandfontein, only those caught on 17/9/37 from St. James. Except in the last column the Numbers are expressed as Percentages.**

Date.	No segmentation visible.	A few cell-divisions.	A good many cell-divisions.	A great many cell-divisions.	Invagination appears.	Distinct division into a yolk-free and a yolk-containing part.	Eye-pigment appears.	Pigment-bands formed.	Strongly pigmented larvae, yolk-masses still fused.	Strongly pigmented larvae, yolk-masses separate.	Hatching.	Hatched.	Total number of batches of eggs examined.
2/5/37	<i>67</i>	..	<i>33</i>	3
18/5/37	5	7	9	<i>25</i>	<i>21</i>	<i>32</i>	44 †
5/6/37	..	8	4	12	15	<i>39</i>	4	4	15	26
24/6/37	..	1	..	2	13	<i>34</i>	5	7	<i>31</i>	5	1	..	82
10/8/37	3	5	3	1	19	<i>44</i>	1	6	10	8	79
24/8/37	2	..	2	9	18	<i>34</i>	5	5	<i>21</i>	2	..	2	44
17/9/37	3	11	3	6	<i>31</i>	<i>46</i>	35
29/9/37	5	..	18	9	18	..	5	27	22
15/10/37	13	13	13	..	13	25	13	13	..	8
25/10/37	15	..	22	7	11	<i>30</i>	11	..	4	27
10/11/37	9	18	..	9	18	9	<i>36</i>	11
29/11/37	11	11	22	11	..	11	..	<i>33</i>	9
13/12/37	..	10	10	10	..	10	<i>30</i>	<i>30</i>	10
30/12/37	17	<i>50</i>	17	..	17	..	6
14/1/38	6	2	2	4	8	<i>40</i>	2	8	<i>21</i>	6	48
31/1/38	6	6	6	18	6	12	<i>35</i>	6	6	..	17
10/2/38	15	23	8	..	15	8	<i>31</i>	13
24/2/38	14	14	..	<i>57</i>	..	14	7
12/3/38	<i>67</i>	<i>33</i>	3
23/3/38
12/4/38
29/4/38	<i>100</i>	2
27/5/38	5	3	..	<i>24</i>	<i>27</i>	<i>38</i>	3	37

* The highest percentages are given in italic figures.

† One crab had degenerated eggs under her abdomen.

a female produces more than one batch of eggs, the incubation-period appears to be about two months under South African winter conditions. This corresponds rather well with the time found for the eggs of berried females which were kept in the laboratory during the period June 1937 to September 1937 (see Table V).

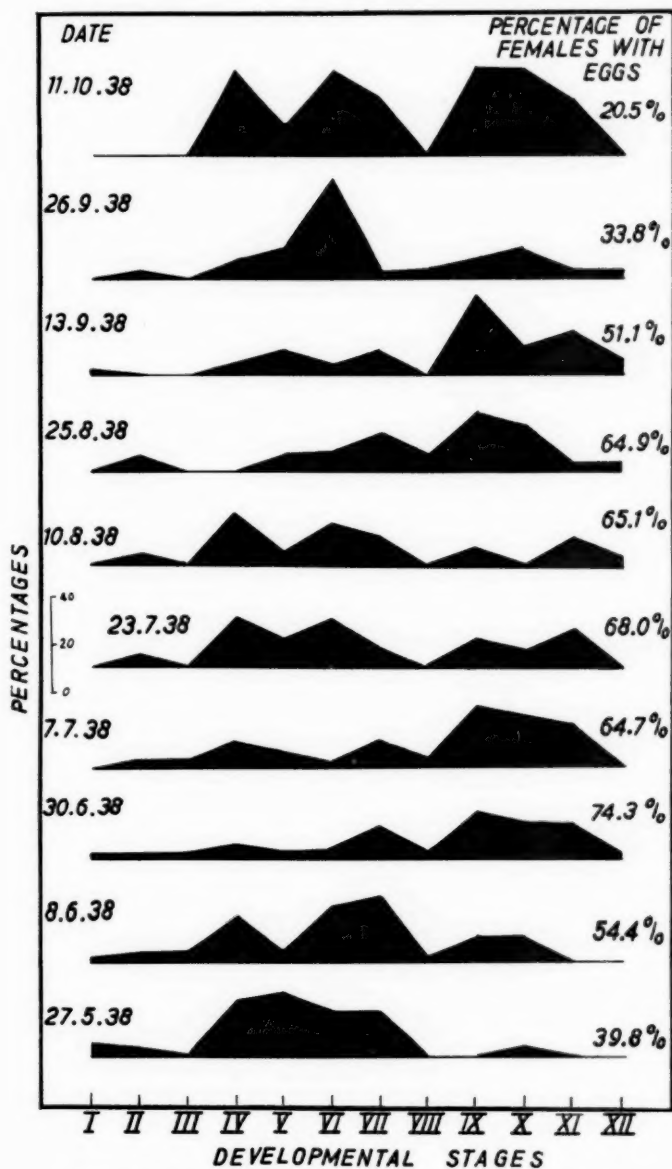


FIG. 4.—The developmental stages of the extruded eggs carried by berried females during the principal breeding-season of 1938.

TABLE V.

Incubation Time for the Eggs of Berried Females kept under Laboratory Conditions during the period June 1937 to September 1937.

Crab.	Average temperature, ° C.	Incubation, time in days.
I	14.5	60
II	14.5	59
III	16.5	56
IV	17.0	53
V	18.5	53

By rearing eggs in the laboratory under *constant* temperatures* it was found that the incubation-period at 16.5° C. is a little over a month, which is shorter than the periods shown in Table V. This is probably to be attributed to the constancy of the temperature, since in the cases recorded in Table V the temperature of the water varied daily, which apparently caused a retardation in the development of the eggs.

As the summer breeding-season lasts for one to two months only, it is likely that few if any of the crabs which ovulate during this period produce more than a single batch of eggs. The probability that a female can produce several batches of eggs in succession makes it likely that one copulation suffices for the fertilisation of the eggs of several egg-batches. This has already been found for other Brachyura (i.e. *Callinectes sapidus*, Rathb.; *Cancer pagurus*, Linn.; *Maia squinado* (Herbst); *Sesarma (Holometopus) cinereum* (Box); *Carcinides (Carcinus) maenas* (Linn.)) (see Gosse, 1852; Williamson, 1900; Churchill, 1917-1918; Duncker, 1934; Broekhuysen, 1936).

During the present investigation four females kept in captivity each extruded a batch of eggs, although no copulation had taken place since the previous batch had hatched and the crab had moulted. The eggs of two of these developed normally, indicating successful fertilisation. In a third the eggs only achieved a somewhat irregular segmentation; in the fourth the early cleavages were normal but the subsequent development was not observed. In another case a female which had been isolated from a very young stage, and therefore had never copulated, extruded a batch of eggs. The eggs, although no fertilisation could have taken place, underwent irregular cleavage but developed no further.

The size at which maturity is reached by the females of this species varies considerably. The smallest berried female in the material collected during the course of the investigation had a carapace-width of 5.5 mm.

* These experiments will be dealt with in a separate paper.

On the other hand the largest female in which the abdomen had not yet attained the mature form had a carapace-width of 11.5 mm. A great deal of individual variation therefore exists.

The Attachment of the Extruded Eggs to the Female Crab.—In *C. punctatus*, and in *Brachyura* in general, each egg of a batch is surrounded by a tightly fitting envelope ending in a twisted strand or funicle which attaches the eggs to an endopodite hair. The eggs are never attached to each other.

The way in which the eggs, after having left the genital pores, become attached to the endopodite hairs of the parent crab has been the cause of much discussion. Broekhuysen (1936), partly as a result of his own observations on *Carcinides (Carcinus) maenas*, Linn., and partly from a study of the facts recorded in the literature, suggested a modification of Williamson's theory (1904). The latter author, working with *Cancer pagurus*, Linn., and *Carcinides (Carcinus) maenas* (Linn.), observed that the eggs, before being attached, were surrounded by a thin wall enclosing a wide cavity which he called the "perivitelline space." Presumably this was formed by absorption of water by the egg shortly after extrusion into the water. Broekhuysen confirmed this observation. The attachment of the eggs to the endopodite hairs is, according to Williamson, effected by each hair acting as a skewer upon which the eggs are impaled. The wall surrounding the perivitelline space is pierced and the egg glued on to the hair by the substance inside the perivitelline space. This substance is liberated into the water, where it hardens to form a new envelope attaching the eggs to the hair; the shape assumed by this envelope is due to the movement of the pleopods acting together with the weight of the eggs. According to Broekhuysen it is probably not a question of the endopodite hair acting as a skewer, but as a result of the periodical movements of the pleopods, these hairs would destroy a part of the wall bounding the perivitelline space by their pressure and liberate the adhesive material. Yonge (1937), working with *Homarus vulgaris* M. Edw., showed that in this species the substance which sticks the eggs to the pleopods, and sometimes to each other, has "properties identical with those of the superficial cuticle of the integument" and is secreted by the cement glands present in the pleopods of the females. According to him this would also hold for the other Decapod Crustacea. It should, however, be stressed that no mention is made of the presence of a perivitelline space in the eggs of *Homarus vulgaris*, which therefore seem to lack this feature.

Twice in the course of the present investigation a female *C. punctatus* was observed in the act of extruding her eggs. The eggs were laid on these two occasions by different females. The crabs were not submerged at the time but were close to the water. When the eggs were examined microscopically it was clear that the perivitelline space was not yet formed

(text-fig. 5). On the first of the two occasions the crab was forced into the water, and many eggs were then seen loosening themselves from underneath the abdomen, indicating that at this stage the eggs were only slightly, if at all, adhesive. A number of eggs transferred to a slide in a drop of sea-water showed a distinct perivitelline space after about an hour. On the other occasion the crab itself was transferred to another dish and prevented from submerging itself (though it was kept moist) for about twelve hours. At the end of this period still no perivitelline space had been formed. The eggs, after having been placed in sea-water, failed to



FIG. 5.—Eggs of *C. punctatus* which had just been extruded, surrounding one of the endopodite hairs. The perivitelline space has not yet been formed.
× 31.

form a perivitelline space of any distinct size, the thin layer surrounding the egg having lost its transparency and having taken on a granulated appearance. On the first occasion the crab was left in the original basin, which had a sloping bottom, part of which was submerged. Some of the eggs (which still did not show a perivitelline space) were transferred to a small dish containing sea-water. The next day these eggs showed a well-developed perivitelline space (text-fig. 6), while the eggs still under the crab's abdomen showed different degrees of attachment (text-fig. 7).

These observations show that in *C. punctatus* the eggs become surrounded by a perivitelline space after having been in sea-water for some time; and that this space is only formed when the eggs become submerged shortly after having been extruded. If they are kept for some time out of water they apparently lose their ability to form a perivitelline space. It is also clear that the perivitelline space contains the substance which glues the eggs on to the endopodite hairs. This supports the present author's statement (Broekhuysen, 1936) that the way in which the eggs become attached to the parent crab show fundamental differences in *Brachyura* and *Macrura*. The origin of the perivitelline space has still to be determined, and it would be very interesting if Yonge's experimental work on *Homarus vulgaris* were repeated with a *Brachyuran* Crustacean.

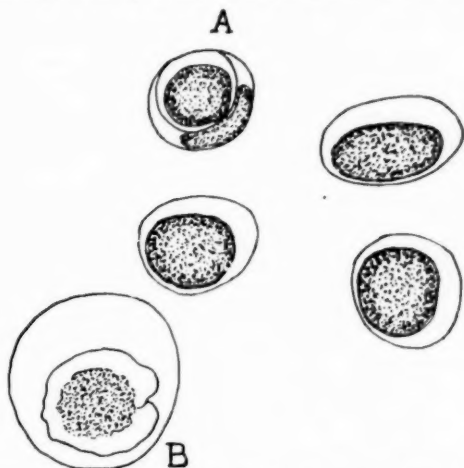


FIG. 6.—Eggs of *C. punctatus* which, after extrusion by the crab, were transferred to a small dish containing sea-water, and which were kept there overnight. A large perivitelline space has been formed. In A a part of the yolk has entered the latter, showing that it really is a space. In B the actual outer envelope was damaged and an abnormally large perivitelline space was formed. $\times 31$.

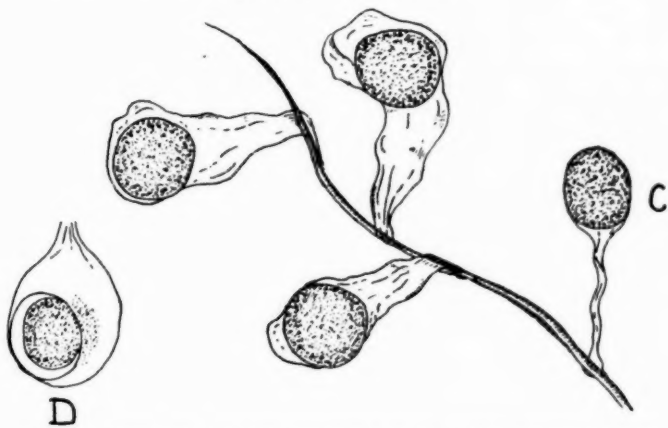


FIG. 7.—Eggs belonging to the same batch of eggs as those represented in the previous figure. In this case, however, the eggs were left under the female's abdomen and examined the next morning, when the drawing was made. The majority of the eggs showed an attachment which was still incomplete. In the figure the three left-hand specimens show this incomplete attachment. In C the attachment is practically complete. In D the actual egg-wall gave way and some of the yolk escaped into the envelope surrounding the egg. $\times 31$.

GROWTH.

Introduction.—In order to obtain information as to the rate of growth, the number of moults, the time required for recovery after moulting, the existence of sexual dimorphism, and the normal length of life, all the crabs brought in from the shore were measured after the sexes had been sorted out. As in the previous section, the index of size employed was the width of the carapace in millimetres. Moreover, the number of crabs which were in the act of moulting or which had recently moulted (indicated by the fact that they were not yet quite hard) was recorded. During the course of the investigation a number of crabs were kept in captivity from a young stage, and their development was followed in order to supplement the data compiled from the material collected on the shore.

Moulting.—In several species of the Decapoda the act of moulting has a double significance, since (a) it is the only period during which growth of the individual is possible, and (b) it is the time at which the female is ready to copulate. In other cases, as for instance in some tropical crabs (see Broekhuysen, 1936, p. 259), it has been found that copulation takes place between individuals which are both in a hard state. As has been mentioned before (p. 339), this also seems to be the case in *C. punctatus*. During the act of moulting and the subsequent period of hardening, the crab is practically defenceless, and many a crab undoubtedly perishes during this phase. This was demonstrated by the fact that in the course of this investigation it appeared to be impossible to rear individuals of this species when several were kept together in the same dish. The ones which moulted were nearly always killed by the others. The first sign that an individual of *C. punctatus* is ready to moult is a decrease in the amount of food taken, which may last for several days. Further, a drab discoloration of the shell becomes noticeable. When moulting has definitely set in, a crack appears in the pleural groove (between notum and pleuron). This is probably due to internal pressure caused by the absorption of water by the tissues. Eventually the carapace is lifted up from the posterior side, while the anterior part acts as a hinge. The soft crab, after having pulled its limbs free from the old shell, escapes from it in a backward direction. In the individuals kept in captivity it was noted that the majority moulted during the night. After the crab has left its old shell a gradual hardening of the newly formed surface-tissue sets in. In *C. punctatus* it seems to be essential, for the normal course of this hardening process, that the crab should be submerged part of the time and exposed to the air for part of it. Many casualties were found to occur in crabs kept constantly submerged, although the basins contained sea-water which was well aerated, while a layer of shell fragments covered the bottom.

In these cases the new shell apparently failed to harden after the crabs had moulted. This is an interesting point which needs further experimental investigation. The time which elapses before a freshly moulted individual becomes hard again seems to be dependent on the size of the individual. It also shows considerable individual variation, probably connected with the physiological condition of the crab at the time of moulting, as is brought out by the data given in Table VI. These data are taken from crabs which were kept in closed dishes containing a thin layer of sea-water with fragments of shell at the bottom. The temperatures are averages of daily temperature readings taken with a maximum and minimum thermometer, which was placed close to the dishes containing the crabs.

TABLE VI.

The Time of Hardening for Crabs of Different Sizes at Different Temperatures. The Time is given in Days, while the Size of the Crabs is given as the Width of the Carapace in Millimetres.

Size of crab in mm.	3	5	7	9	11	13	15	17	19	21	23
Temperature, ° C.											
14		2					6				
14.5				4, 3							
15			2		6, 5	4, 5				6	
15.5			2, 2, 4	3		4			9	10	
16		3, 2	2				7	8		7	
16.5		2				6	4		8		
17		3, 3	2, 3, 1		3		6, 5	6, 10			
17.5			2, 2	3, 4	2, 2		6		3		
18		2-3, 1	1-2, 2, 2			6, 6	5-6	6, 5		5	
18.5		2, 2, 1		2	2	4					
19						3	6	5-6	6, 6, 7		
19.5		2-3	2, 1, 1			5-6					
20		2	2, 2	2	3	3	5	4	5		
20.5		1	2-3, 2	2, 2, 1	1	4-5, 3, 4-5	5	4		4, 6	
21		2-3, 1-2	2	2, 3-4, 2	3	3, 4	5, 5	5	4-5, 5		
21.5	1, 1	1	1	2-3, 2-3, 2	1		2	9	9		5, 7
22		1-2, 2	1, 1		2-3		4	4, 5	8		
22.5		1, 2	2			4	6				7
23			1			4-5					6
23.5					2			7			
24					2						
25		1									
Averages	1	2	2	2.5	2.5	4.5	5	6	6.5	6.5	6.5

As may be seen from the above table, temperature does not seem to play an important rôle in the hardening process. The larger the individual, however, the longer the time of hardening.

In many of the Crustacea from temperate regions whose life-histories have been studied, it has been found that moulting occurs most frequently in the warmer part of the year. During the winter a definite decrease in moulting activity takes place, while in some cases moulting comes to a dead stop. In a few cases (see Broekhuysen, 1936, p. 363) a difference exists between the time of the height of the moulting season of the males and that of the females, the former being reached earlier in the season than the latter. The explanation for this probably is that (a) the chief breeding-season of many Crustacea falls in the winter, when a great many of the females are in berry. These eggs must hatch before moulting takes place.* When the incubation-time is considerable, which is often the case because of the low water-temperatures, the first moult of the females after the winter-season may consequently be postponed; (b) in species in which copulation only takes place between a hard male and a female that has just moulted and is still soft, much of the reproductive capacity of the species would be lost if the height of the moulting season fell in the same period for both the sexes. In that case individuals of both sexes would be soft at the same time, which would probably reduce the number of copulations considerably.

In order to find out whether there is any seasonal periodicity in the moulting activities of *C. punctatus*, the number and percentage of crabs which had recently moulted, in the monthly catches, over the period of a year, have been set forth in Table VII and expressed graphically in text-fig. 8. In this figure monthly averages of the water-temperature at Muizenberg have been included, as well as the atmospheric temperature at Wingfield Aerodrome and the Simonstown Dockyard. These are the nearest places at which temperature readings are carried out.†

* During the whole period of this investigation, it happened twice only that a crab moulted before all the eggs had disappeared from underneath the abdomen. This must be considered as being very rare in Crustacea, as the present author has neither found it mentioned in the literature nor met with it during his investigation on *Carcinides (Carcinus) maenas* (Linn.) (Broekhuysen, 1936).

† The water-temperatures have been compiled by Dr. W. E. Isaac from the available water-temperature readings over the period 1932 to 1936. There is definite evidence which makes it very likely that the average water-temperature at Strandfontein is somewhat higher than that at Muizenberg. As, however, actual temperature-readings for the former locality are not available, the latter must suffice. The atmospheric temperatures for Wingfield Aerodrome are very accurate, as they are compiled from hourly day and night readings; the temperatures for Simonstown Dockyard are not very accurate, as readings are carried out only once a day (early in the morning). The value of these temperatures is limited, as local conditions may have a considerable effect.

TABLE VII.

Number and Percentage of Females and Males which had recently Moulded in the Material collected in False Bay over the period May 1937 to May 1938.

Month.	Males.		Females.	
	Number.	Percentage.	Number.	Percentage.
May	0	0.0	4	4.0
June	1	1.1	1	2.3
July
August . . .	14	5.5	2	2.4
September .	19	15.7	7	4.8
October . .	48	15.7	17	8.5
November .	31	12.0	46	13.3
December .	18	9.6	19	7.9
January . .	18	8.9	34	12.5
February .	40	16.1	49	17.1
March . . .	28	14.1	64	16.5
April . . .	34	17.3	45	16.9

From this table and figure it will be seen that there is a seasonal periodicity in the moulting activity of the crab under consideration. The spring and summer is the period of the year during which moulting takes place most frequently in both the sexes, while this activity is decreased to a minimum during the winter months.* Fig. 8 further reveals a distinct difference between the times at which the two sexes show a marked increase in moulting activity in the spring. The males had already reached their maximum in such activity in September 1937, while the females did not reach that stage until November 1937. The explanation of this difference is very probably that mentioned under (a) on p. 350, because, as has already been noted (see text-fig. 3), September and a part of October still fall in the chief breeding-season of the females. This consideration probably also explains the more gradually sloping character of the curve in

* On the days when collections were made in the months November 1937, February 1938, and March 1938, shells of *Cyclograpsus* were found to be left behind in the intertidal pools, at Strandfontein, during low water. Of these a certain number were damaged in such a way that the sex could not be determined. There were, however, a fair number whose sex could be made out, and the proportion of casts of each sex present also indicates that during the summer months moulting takes place in both sexes to about the same extent. The figures were as follows: November, 49 males, 34 females; February, 53 males, 79 females; March, 71 males, 90 females.

+ AIR-TEMPERATURE WINGFIELD
 • AIR-TEMPERATURE SIMONSTOWN
 WATER-TEMPERATURE
 --- FEMALES
 --- MALES

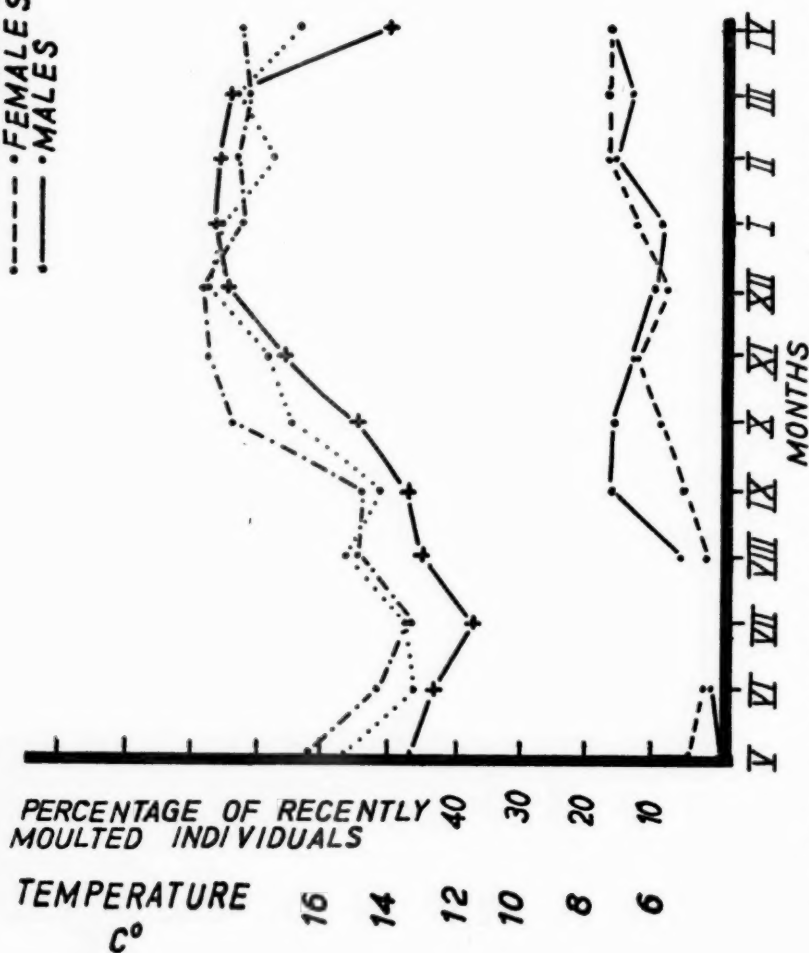


FIG. 8.—Seasonal periodicity in the moulting-activities of *C. punctatus* in False Bay, compared with the seasonal change in temperature of the water and the atmosphere at the nearest places where such data are recorded. The data referring to the moulting-activities cover the period May 1937 to April 1938, while the average water temperatures cover the period 1932 to 1934.

the case of the females in comparison with that of the males. The percentage of crabs which had recently moulted appears to be rather low, even in the months during which moulting activity is maximal. This is probably due to the fact that the hardening process only takes a few days (see Table VII), and therefore crabs which moulted about a week (or even less in the case of the smaller individuals) previous to the date of collection have lost all sign of their recent moult.

In order to check the findings just described, the number of moults, and the months in which they took place, of all the crabs kept in captivity during the course of this investigation, have been combined in Table VIII and these data have been graphically expressed in fig. 9.

TABLE VIII.

The Number of Moults in the Different Months of the Year for all the Crabs kept under Laboratory Conditions during the period March 1937 to January 1940.

Month.	Males.			Females.		
	Number of moults.	Percentage which these moults form of total number of moults observed.	Total number of crabs kept in captivity.	Number of moults.	Percentage which these moults form of total number of moults observed.	Total number of crabs kept in captivity.
May	1	1.3	22	2	1.5	44
June	5	6.6	22	7	5.1	50
July	4	5.3	22	3	2.2	49
August	7	9.2	22	8	5.8	53
September	5	6.6	20	15	11.0	52
October	11	14.5	21	19	13.9	57
November	4	5.3	19	18	13.1	51
December	9	11.8	20	15	11.0	45
January	3	4.0	21	11	8.0	47
February	7	9.2	19	13	9.5	43
March.	12	15.8	21	22	16.0	32
April	8	10.5	23	4	2.9	30
Total number of moults	76			137		

When Table VII and text-fig. 8 are compared with Table VIII and text-fig. 9, it will be seen that they agree so far as the seasonal periodicity of the moulting activity is concerned. In the case of the crabs kept in the laboratory this periodicity is less distinct than in the crabs from the shore, but this might be expected, on account of the more uniform temperature conditions in the laboratory and the smaller number of available data. The data obtained on the crabs in captivity reveal no difference in the rate of moulting between males and females at the beginning of

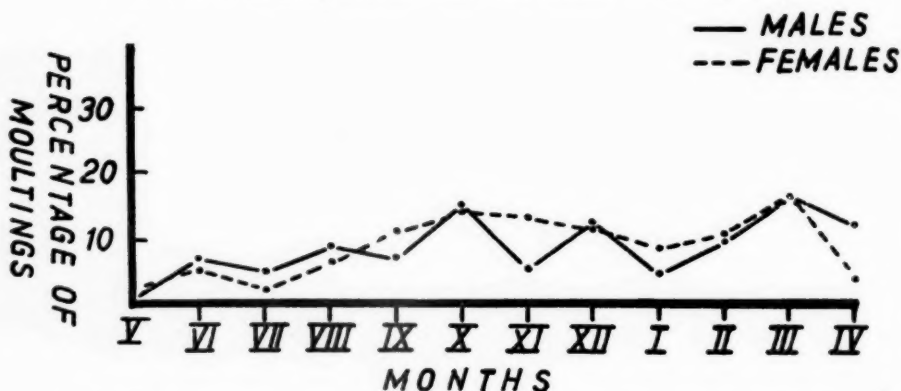


FIG. 9.—The percentage of moults which occurred in the different months among crabs kept under laboratory conditions during the period March 1937 to January 1940.

the moulting-season, such as was found for the crabs on the shore. This is probably due to the fact that comparatively few of the crabs in captivity produced eggs, and the retardation of moulting of the females was therefore much less evident than in the crabs in their natural habitat.

Sexual Dimorphism.—In *C. punctatus*, as in practically all Brachyura, female and male individuals show differences in the shape and structure of the abdomen and the pleopods, both of which are adapted to the different functions connected with reproduction. Moreover, the chelipeds in the males are more strongly developed than in the females (see Pl. LVI, fig. 2). In order to determine whether there is any consistent difference in size between the individuals of the two sexes, the number of crabs of each size, among the 5803 individuals which had been measured during the course of the investigation, was plotted, and the result is given in text-fig. 10. In this figure three different curves are shown. Two of these apply respectively to the two sexes, while the third applies to the ovigerous females only. From this figure it will be seen that, as far as size is concerned, there is very little, if any, difference between males and females. The

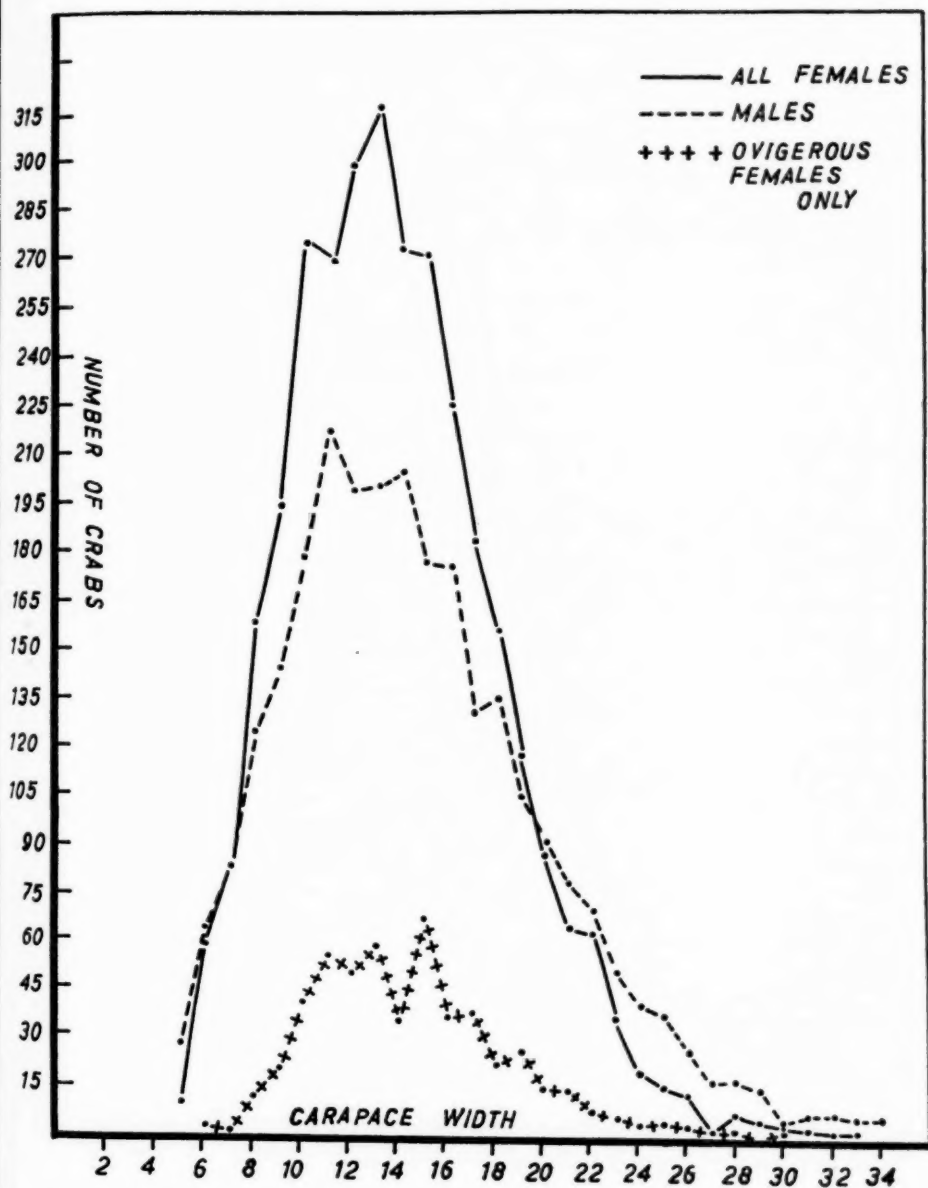


FIG. 10.—The distribution of all the crabs measured over the different size-classes. The size is expressed as carapace-width in mm.

only difference which is brought out by the figure is that among the crabs with a carapace-width of over 22 mm. more males were collected than females, although the reverse was true for the smaller crabs. This indicates that a somewhat larger number of males than females reach these larger stages. Fig. 10 also shows that the extruding of eggs is not confined to a particular size-group but takes place in individuals in which the carapace-width varies from 6 mm. to almost 30 mm.

The Rate of Growth.—As the crabs can only increase their size after, or better during, the act of moulting, the rate of growth is dependent upon I. the number of moults, and II. the amount of increase in size after a moult has taken place. As there seems to be no significant difference in size between the two sexes, these need not be treated separately in this connection.

I. In Table IX the intervals between two successive moults and the average of the daily temperature-readings for each interval, for crabs kept under laboratory conditions, are given.

As will be seen from this table, the temperature proves to have little, if any, influence on the length of the interval between two moults in crabs of about the same size, kept under laboratory conditions. This seems to be somewhat inconsistent with the conclusion arrived at on p. 351, namely, that there is a seasonal periodicity in the moulting activity of this species, such activity being at its maximum during the summer months. This presumably indicated an influence of temperature. It should, however, be noted that the feeding of the crabs kept in the laboratory took place at the same rate in summer and winter, and that the food was actually *given* to the crabs. In their natural habitat these crabs have to hunt for their food, and it is likely that the lower temperatures in winter decrease their activities, thus causing a decrease in the amount of food consumed, which, together with the reduced metabolism, would result in a decrease in the rate of growth and in the moulting activity. Moreover, as has been pointed out before, only very few of the females kept under laboratory conditions (most of which were kept apart from males) produced an egg-batch. Therefore in these cases the moulting activity was not interrupted by the carrying of eggs, which under natural conditions has been shown to affect the time of moulting. Further, it should be kept in mind that the chief breeding-season of this species comes to an end in September and October. During the spring and the summer, therefore, the crab population is on the average younger than in the winter (see also text-fig. 11); and from what we know of the correlation between the length of the interval between two moults and the size of the crab, moulting should occur more frequently in summer than in winter. Thus, even though the duration of the interval between two moults is not directly dependent upon the

TABLE IX.

The Length of the Interval between Two Successive Moults in relation to Temperature and to the Size of the Crabs. The Temperature is given in $\frac{1}{2}^{\circ}$ C., the size of the Crab as Carapace-width in mm., and the Interval in Days.

Size of crab.	Temperature to the nearest $\frac{1}{2}^{\circ}$ C.												
	16	16.5	17	17.5	18	18.5	19	19.5	20	20.5	21	21.5	22
	Interval between two successive moults in days.												
5	23	32	17
													29
													29
6	54	..	34	..	33	41
										40			30
7	57	44	36	..	50	40	..
				38							39		
8	73	..	76	76	60	46	57
						69							
9	..	141	69	44	..
												67	
10	62	74	..	78	105	82	..
11	63	94	125	85
							60						
12	87	..	154	58	58
	98												86
13	72	25	..	63	79
14	100	106	..	73	74	77
				68			104						53
15	117	38	115	111	61
				191									
				56									
16	..	120	..	29	79	89	..
												130	
17	207	..	151	..	142	126	..	84
											93		
18	112	45
19	222	243	97	..	83	..	77
20	184	142	79	..	94
21	220
22	148	242	..	257	180
23	126	171
								90					
24	272
25	244	221

prevailing temperature, the existence of a more or less definite seasonal periodicity in the moulting activity of the crabs in their natural habitat seems to be understandable.

II. In order to determine the amount of the increase in size which occurs after each moult, in crabs of different sizes, all the relevant information obtained in the course of this investigation has been summarised in Table X. Those cases in which crabs lost one or more limbs before moulting took place have also been included in order to increase the number of observations. As the increase in size after a moult is somewhat reduced when limbs have to be regenerated, the data presented in Table X must therefore be considered as being slightly on the low side.

TABLE X.

The Amount of Growth in Crabs of Different Sizes.

Carapace-width before moulting, in mm.	Average increase in carapace-width, in mm.			Individual variation in increase of size, in mm.			Average increase as percentage of original carapace-width.			Number of observations.		
	Females.	Males.	Females and males.	Females.	Males.	Females and males.	Females.	Males.	Females and males.	Females.	Males.	Females and males.
4	0.8	0.9	0.8	0.6-0.9	..	0.6-0.9	20	23	20	3	2	5
5	1.0	0.8	0.9	0.7-1.4	0.6-1.1	0.6-1.4	20	16	18	5	5	10
6	1.0	1.1	1.1	0.8-1.2	0.5-1.8	0.5-1.8	17	18	18	6	11	17
7	1.5	1.3	1.4	1.1-1.8	0.9-1.9	0.9-1.9	21	19	20	8	8	16
8	1.5	1.7	1.6	1.2-1.8	1.4-1.9	1.2-1.9	19	21	20	4	5	9
9	1.6	1.7	1.6	1.3-1.9	1.4-2.0	1.3-2.0	18	19	18	3	5	8
10	1.9	2.1	2.0	0.8-2.2	1.4-2.3	0.8-2.3	19	21	20	6	6	12
11	2.0	1.9	2.0	0.9-2.7	1.7-2.1	0.9-2.7	18	17	18	3	3	6
12	2.1	2.5	2.2	1.7-2.8	1.9-2.8	1.7-2.8	18	18	18	9	5	14
13	2.0	2.4	2.2	1.2-2.8	2.2-2.6	1.2-2.8	15	19	17	6	4	10
14	2.2	..	2.2	0.9-3.1	..	0.9-3.1	15	..	15	8	0	8
15	1.9	2.7	2.3	1.8-2.5	2.6-2.9	1.8-2.9	13	18	15	7	6	13
16	2.3	0.1	2.1	1.5-3.4	..	0.1-3.4	14	1	13	11	1	12
17	2.3	2.6	2.4	1.0-3.0	2.0-2.9	1.0-3.0	14	15	14	6	3	9
18	2.3	1.8	2.2	1.6-3.6	1.5-2.0	1.5-3.6	13	10	12	5	2	7
19	2.1	..	2.1	0.4-3.0	..	0.4-3.0	11	..	11	10	0	10
20	2.4	2.5	2.4	1.8-3.3	1.8-3.2	1.8-3.3	12	13	12	7	2	9
21	1.9	..	1.9	1.3-2.5	..	1.3-2.5	9	..	9	3	0	3
22	1.4	2.6	1.7	0.8-2.2	..	0.8-2.2	6	12	8	3	1	4
23	1.9	..	1.9	1.7-2.1	..	1.7-2.1	8	..	8	3	0	3
24	1.3	1.0	1.2	1.0-1.5	..	1.0-1.5	5	4	5	3	1	4
25	2.2	..	2.2	1.9-2.4	..	1.9-2.4	9	..	9	4	0	4

From this table we may conclude that on the whole the percentage increase in size after each moult shows a gradual decrease as the crab grows larger. Up to a carapace-width of about 12 mm. the periodical percentage increase in size seems to be almost constant, but from that point onwards a definite decrease is noticeable. From that part of the table which gives the individual variation it will be seen that this can be considerable.

In order to obtain information about the age of these crabs, the percentage of crabs of a particular size was plotted against the different sizes in mm. for each month of the year for both the sexes. The results are given in text-fig. 11.* Owing to the fact that even mature crabs moult several times a year in this species, and because of the great individual variation which was found to exist, no definite year-classes can be made out in this figure. The figure does bring out, however, the existence of a maximum of individuals of the smaller size-classes during the spring and summer months,† while during the autumn and winter months the different size-classes are more evenly distributed and the percentages of crabs of the largest size-classes are somewhat higher. Hence it appears to be very difficult, if not impossible, to draw any conclusions about the age reached at any particular size by the majority of the crabs, as well as about the extreme duration of life, from the data obtained by measuring crabs collected along the shore at random.

When the rate of growth of the crabs which were kept in the laboratory is compared with the data given in text-fig. 11, some estimation of the age which the crabs on the shore reach can be made. It should, however, be borne in mind that this estimate cannot be very exact and will represent

* In addition to the data given in this figure, which only includes those crabs whose sex could be determined without dissection, the following crabs of externally undeterminable sex and with a carapace-width not exceeding 7 mm. were recorded.

Month.	Number.	Month.	Number.	Month.	Number.
June 1937	4	October 1937	0	January 1938	8
August 1937	11	November 1937	1	February 1938	10
September 1937	5	December 1937	0	April 1938	2

† It will be noticed that the data for September 1937 appear to be somewhat out of order when compared with the previous and the following months. These data, however, refer to material collected at St. James on the 17th (95 ♀♀ + 111 ♂♂) and at Strandfontein on the 29th (107 ♀♀ + 121 ♂♂). The latter collection was made while the water was extraordinarily high, which made it possible to collect only the crabs occurring at the highest intertidal levels. This may have resulted in many of the smaller ones being overlooked.

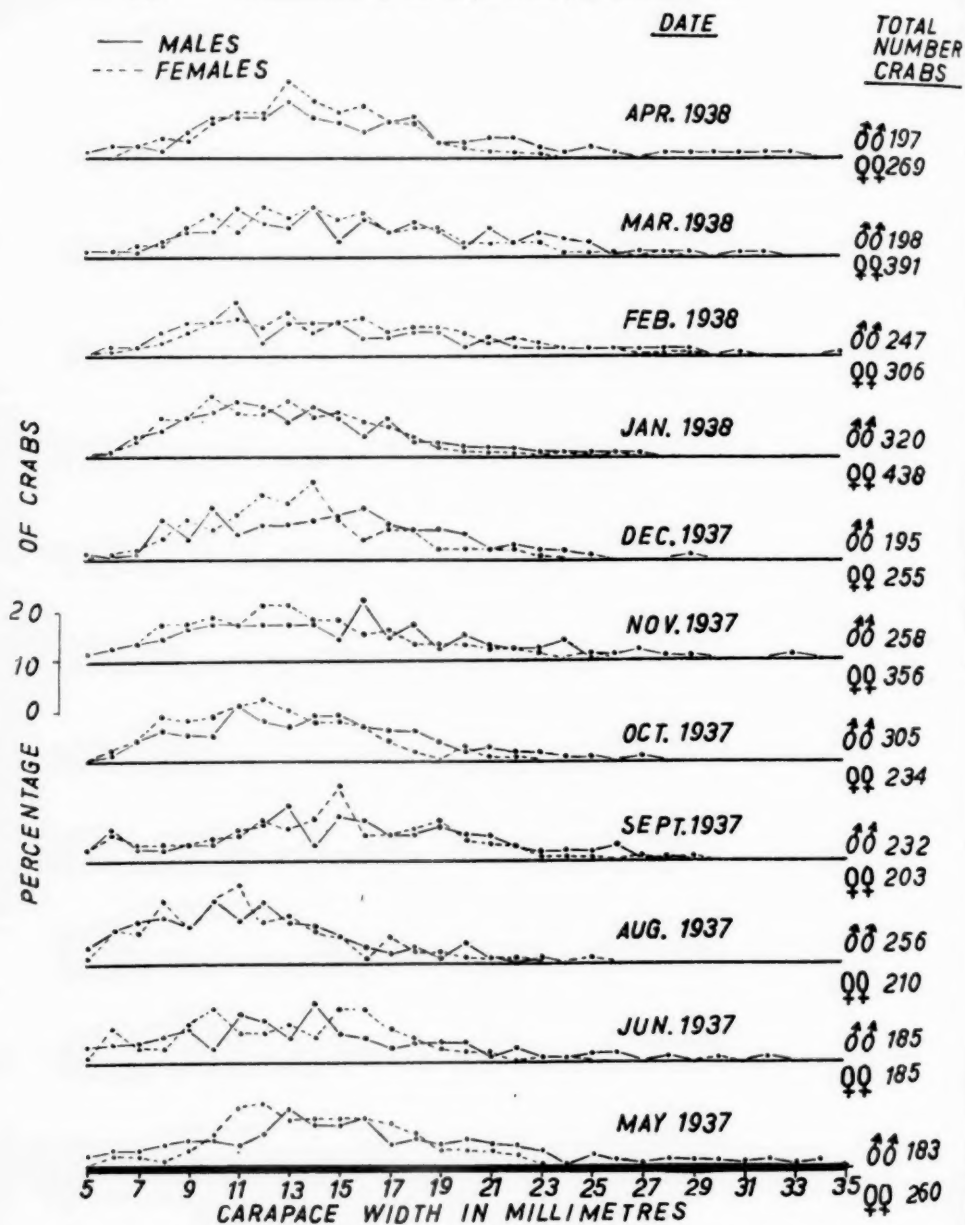


FIG. 11.—The distribution of the crabs of different sizes in the different months of the period May 1937 to April 1938. No observations are available for July 1937.

a minimum value, as the rate of growth under laboratory conditions will very likely be higher than in crabs living under natural conditions, owing to the more extreme temperature and food conditions in the latter. In Table XI the rate of growth of all the crabs which, when collected, had a carapace-width smaller than 7 mm., and which were kept in the laboratory for longer than a year, is presented.

TABLE XI.

The Rate of Growth in Crabs kept under Laboratory Conditions.

Crab.	Period during which crab was kept in captivity.	Size in mm. at the beginning.	Size in mm. at the end.
♂ 1.	1 year and 7 months	4	18
♂ 2	1 " " 6 "	4	19
♂ 3	1 " " 5 "	5	17
♂ 4	1 " " 6 "	5	18
♂ 5	1 " " 10 "	6	20
♂ 6	1 " " 6 "	6	>18
♂ 7	1 " " 3 "	6	18
♂ 8	1 " " 2 "	6	20
♀ 1	1 " " 2 "	5	22
♀ 2	1 " " 3 "	6	22
♀ 3	1 " " 4 "	7	22
♀ 4	2 " " 1 "	7	21

These observations show that the crabs with a carapace-width of about 17 to 22 mm. can be considered as being at least in their second year of age. Text-fig. 11 shows that the bulk of crabs found on the shore in False Bay have a carapace-width varying between 6 and 22 mm. As the crabs continue to increase in size after each moult, even after a carapace-width of 22 mm. has been attained (see Table X), the majority of individuals of this species in False Bay seem to reach an age of approximately two to three years, after which most of them apparently die or get killed. The data given in Table IX indicate that the individuals which have reached a carapace-width of over 22 mm. only moult once or twice a year when kept in the laboratory. As the data in Table X indicate that the increase in size after each moult for crabs with a carapace-width of about this size is approximately 2 mm., crabs with a carapace-width of about 28 mm. must be in their third or fourth year, while the few individuals which were found to have a carapace-width of more than 28 mm. will probably be at least in their fifth year. As has been mentioned before (see p. 356), rather more males than females seem to reach these older ages.

THE SEX-RATIO.

Of all the crabs collected at random on the False Bay coast during the course of this investigation, 2613 or 45 per cent. proved to be males, and 3190 or 55 per cent. were females. It therefore appears that among the population of *C. punctatus* in this bay the females were numerically somewhat stronger than the males in the years 1937-1938. This fact is also brought out by the data presented in text-fig. 11. From these it will be seen that in eight of the eleven months in which crab-material was collected the females outnumbered the males.

DISCUSSION.

As has been pointed out in the introduction to this paper, one of the aims of studying the life-history of *C. punctatus* in a southern temperate region was to make it possible to compare the results with those which were obtained by the same author in his study of the life-history of *Carcinides* (*Carcinus*) *maenas* (L.) in the coastal waters of Holland (Broekhuysen, 1936). This comparison is of interest as it concerns two species which are very similar to one another, which both frequent the intertidal zone,* and of which one occurs in a southern temperate region while the other is found in a northern temperate region.

When the results which have been described on previous pages are compared with what has been found for *C. maenas*, a very close correspondence between the two species becomes evident as regards breeding or growth. In the activity of the gonads of the females a definite periodicity was found to exist in both these species. The females of both have their chief breeding-season during the winter. In *C. punctatus* it covers the period May to November and in *C. maenas* it occurs in the period between November and June. The correspondence in length and date is very striking. In the case of the southern crab several egg-batches appear to be extruded in close succession during this breeding period, as the winter is mild with fairly high water-temperatures.† In the northern region, where the winters are much more severe, the development of the eggs takes so long that only one egg-batch is extruded. In both species

* It must be stressed here, that at the locality where *C. maenas* was studied, this species was more a sublittoral than an intertidal species, although it was far from rare between tidemarks. The majority of individuals of *C. punctatus* are found in the higher parts of the intertidal zone. Therefore there is some difference between the habitats occupied by these two species.

† It should be noted that although the southern winter is relatively mild, it is by no means the same in temperature throughout the region inhabited by *C. punctatus*. The mean annual surface temperature round the South African coasts varies from not much more than 12° C. in the west to more than 20° C. in the east.

a second, minor, breeding-season was found to occur in the summer (in January in *C. punctatus* and in July in *C. maenas*). In the case of the males a striking difference between the two species seems to exist. In *C. punctatus* a definite periodicity in the gonad-activity of the males was found, adapted to the periodicity in the gonad-activity of the females. In *C. maenas* no such periodicity was found, and the males of this species seemed to be fit for copulation throughout the year.

As far as the incubation period of the eggs is concerned, it was found that at an average temperature of about 14.5–18.5° C. with a daily variation in temperature, the eggs of *C. punctatus* hatched after nearly two months. The incubation period for the eggs of *C. maenas*, at an average temperature of 16.5° C. with daily variation, has proved to be a little over a month. When the eggs of *C. punctatus* were kept at a constant temperature of 16.5° C. their incubation time was reduced to a little over a month. From this it seems likely that the incubation period of *C. punctatus* is somewhat longer than that of *C. maenas*, while variation in temperature seems to retard the development of the eggs.

When moulting is considered, a difference between the two species is found, as the majority of the mature individuals of *C. punctatus* still moult more than once a year, while in *C. maenas* mature individuals moult only once a year. This difference has very likely something to do with the milder climate inhabited by the former species, as moulting-activity never comes to a complete standstill in *C. punctatus*, while in *C. maenas* it decreases almost to zero during the coldest months of the European winter. In both species, however, a seasonal periodicity in the moulting-activity was found to exist, with a maximum during the summer. In *C. punctatus* no actual difference in season between the moulting-periods of the two sexes seems to occur, although the males reach their maximum somewhat earlier in the summer than the females, while in the other species there is a definite seasonal difference between the moulting-periods of the two sexes. This may have something to do with the fact that in *C. punctatus* copulation seems to take place between two hard individuals, while in *C. maenas* the females are only fit for a successful copulation when they have just moulted and are still soft. The time required for hardening after moulting has taken place is of about the same order in both species. The percentage increase in size after a moult seems to be somewhat smaller in the case of *C. punctatus*, which corresponds with its smaller size. Moreover, in *C. punctatus* there is a noticeable decrease in the amount of the increments as the individual grows larger, while in the other species the increments remain approximately constant. A further difference between the two species is that in *C. punctatus* the average size of individuals of both sexes is the same, while in *C. maenas* the males are larger than the females.

As far as age is concerned there is reason to believe that there is considerable correspondence between the two species. In *C. punctatus* the majority of the individuals seem to attain an age of two to three years, while a smaller number reach three to four years, and a few five years. In *C. maenas* the majority appeared to reach three years, while a small number reach four and a few five years.

We are presented, therefore, with two crabs whose life-histories show a marked degree of correspondence, a correspondence which is presumably correlated with the occurrence of similar combinations of environmental conditions in the northern and southern hemispheres respectively.

SUMMARY.

1. The investigation deals with a small crab, *Cyclograpsus punctatus*, inhabiting the higher parts of the intertidal zone, and distributed along the South African coast from Port Nolloth to Natal. The material studied was collected in False Bay.

2. The investigation refers to the period May 1937 to January 1940.

3. During this period *C. punctatus* showed a principal breeding-season in winter and a subsidiary one in summer, though a limited amount of breeding continued throughout the year. In both breeding-seasons the period of maximal activity for the females fell a little later than that for the males, the one being adjusted to the other.

4. Evidence is given supporting the view that the female *Cyclograpsus* extrudes several batches of eggs during the principal breeding-season.

5. The eggs appear to be attached to the endopodite hairs of the pleopods of the female by an adhesive substance derived from the perivitelline space of the egg itself. This is probably in contrast to the method occurring in the *Macrura*, but agrees with that found in other *Brachyura*.

6. The development of the eggs was followed, and twelve developmental stages, similar to those of other *Brachyura*, are described.

7. The act of moulting is described. The rate of hardening of the new carapace seems to be little affected by temperature, but the longer the crab the longer it takes. Temperature appears to have little influence on the length of the interval between two moults in crabs of the same size, at least under laboratory conditions.

8. While a few of the crabs will moult at any time of the year, the majority moult in spring and summer.

9. The spring increase in frequency of moulting is more rapid for males than for females. Probably this is because the number of berried females is highest in winter, and they do not usually moult until the eggs have hatched.

10. The percentage increase in size of the crabs after each moult shows a gradual decrease as the crab grows larger.

11. It is estimated that the majority of individuals of *Cyclograpsus* reach an age of two to three years (probably attaining a carapace-diameter of approximately 20 mm. during their second year), a smaller number living for three to four years and a few for five.

12. There are the usual Brachyuran sexual differences between the male and female *Cyclograpsus*; but there is no significant difference between the average sizes of the sexes.

13. Sex-ratio: of 5803 individuals examined, 2613 were males and 3190 females.

14. The life-history of *Cyclograpsus punctatus* is compared with that of *Carcinides maenas*. It is shown that although not identical they are very similar, and that the two crabs are ecologically comparable forms inhabiting similar environments in different hemispheres.

ACKNOWLEDGMENTS.

I have pleasure in thanking Professor T. A. Stephenson and Dr. H. Sandon for reading the manuscript and giving their criticism.

I am also indebted to the Meteorologist of Wingfield Aerodrome, Cape Town, and the authorities of the Naval Dockyard at Simonstown, for allowing me to make use of their temperature records.

REFERENCES.

- BALSS, H., "Crustacea. VII: Decapoda Brachyura," Michaelsen, Beitr. Kenntnis Meeres-fauna West Afrikas, iii, 3, 1922.
BALSS, H., "Crustacea," Kükenthal's Handbuch der Zoologie, iii, 1, 1927.
BROEKHUYSEN, G. J., "On Development, Growth and Distribution of *Carcinides maenas* (L.)," Arch. Néerl. Zool., ii, 257-399, 1936.
BRIGHT, K. M. F., "The South African Intertidal Zone and its Relation to Ocean Currents. II. An Area on the Southern Part of the West Coast. III. An Area on the Northern Part of the West Coast," Trans. Roy. Soc. S.A., xxvi, 1, 1938.
CHURCHILL, E. P., Jr., "Life History of the Blue Crab," Bull. U.S. Bur. Fisher., xxxvi, 1917-1918.
DUNCKER, G., "Gefangenschaftsbeobachtungen an *Sesarma cinerea*, Milne Edw.," Zool. Jahrb. Syst., lxi, 285-290, 1934.
EYRE, J., BROEKHUYSEN, G. J., CRICHTON, M. I., "The South African Intertidal Zone and its Relation to Ocean Currents. VI. The East London District," Ann. Natal Mus., ix, 1, 1938.
GILCHRIST, J. D. F., "Larval and Post-larval Stages of *Jasus lalandii*," Journ. Linn. Soc. Zool., xxxii, 1916.
GILCHRIST, J. D. F., "Crawfish Investigations, including Experimental Hauls, Artificial Rearing and Migratory Movements of the Cape Crawfish (*Jasus lalandii*)," Mar. Biol. Rep. S.A., iv, 1918a.

- GILCHRIST, J. D. F., "The Cape Lobster and the Cape Crawfish or Spiny Lobster," Mar. Biol. Rep. S.A., iv, 1918 b.
- GILCHRIST, J. D. F., "A Post-puerulus Stage of *Jasusalandii*," Journ. Linn. Soc. Zool., xxxiv, 1920.
- GOSSE, P. H., "On the Sloughing of the Spider-Crab (*Maia squinado*)," Ann. Nat. Hist., ii, 10, 1852.
- KOESCHELT, E., and HEIDER, R., "Lehrbuch der Vergleichende Entwicklungsgeschichte der Wirbellosen Thiere," 1893, 1909, and 1910.
- RATHBUN, M. J., "The Grapsoid Crabs of America," Smithsonian Inst., U.S.A., Nat. Mus. Bull., xcvii, 1918.
- STEPHENSON, T. A., STEPHENSON, A., DU TOIT, C. A., "The South African Intertidal Zone and its Relation to Ocean Currents. I. A Temperate Indian Ocean Shore," Trans. Roy. Soc. S.A., xxiv, 1937.
- STEPHENSON, T. A., STEPHENSON, A., BRIGHT, K. M. F., "The South African Intertidal Zone and its Relation to Ocean Currents. IV. The Port Elizabeth District," Ann. Natal Museum, ix, 1, 1938.
- VON BONDE, C., MARCHAND, J. M., "The Natural History and Utilization of the Cape Crawfish, Kreef, or Spiny Lobster (*Jasusalandii*)," Fish. Bull. No. 1, Fish. Mar. Biol. Survey S.A., 1935.
- VON BONDE, C., "The Reproduction, Embryology and Metamorphosis of the Cape Crawfish," Fish. Bull. No. 1, Fish. Mar. Biol. Survey, vi, 1936.
- WILLIAMSON, H. C., "II. Contributions to the Life-History of the Edible Crab (*Cancer pagurus*, Linn.)," 18th Rep. Fish. Board for Scotland, iii, Sci. Invest., 1900.
- WILLIAMSON, H. C., "II. Contributions to the Life-History of the Edible Crab (*Cancer pagurus*) and of other Decapod Crustacea: Impregnation; Spawning; Casting; Distribution; Rate of Growth," 22nd Rep. Fish. Board for Scotland, iii, Sci. Invest. 1904.
- YONGE, C. M., "The Nature and Significance of the Membranes surrounding the developing Eggs of *Homarus vulgaris* and other Decapoda," Proc. Zool. Soc. London, A, cvii, 4, 1937.

EXPLANATION OF THE PLATES.

PLATE LVI.

- Fig. 1. The habitat of *Cyclograpsus punctatus* at Strandfontein. As can be seen, the intertidal rock is very much broken up here. The formation consists of pieces of fairly soft sandstone, in and under which many of these crabs were found.
- Figs. 2 and 3. Male and female of *C. punctatus*. $\times \frac{1}{2}$.

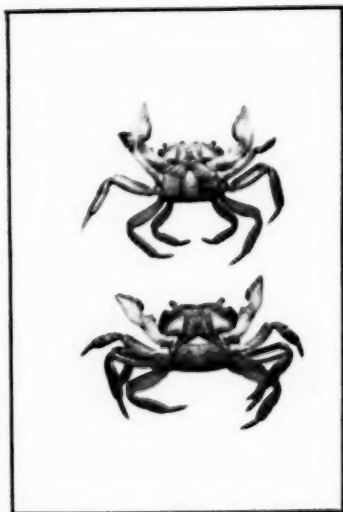
PLATE LVII.

Developmental stages of the eggs of *Cyclograpsus punctatus*. $\times 33$.

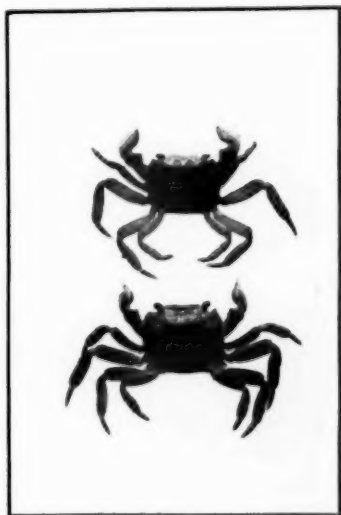
- Fig. 1. Eggs which show early cleavages. A, endopodite hair.
- Fig. 2. First appearance of a yolk-free part (B), or beginning of invagination.
- Fig. 3. Distinct yolk-free (B) and yolk-containing parts (C).
- Fig. 4. Strongly pigmented larvae. Only two small separate yolk-masses (C) remain. D, eye-pigment.
- Fig. 5. Nearly hatched larvae (prezoea, except for G, which is a zoea just emerging from the prezoea cast). E, skin of prezoea; F, egg-capsule.
- Fig. 6. Zoea.



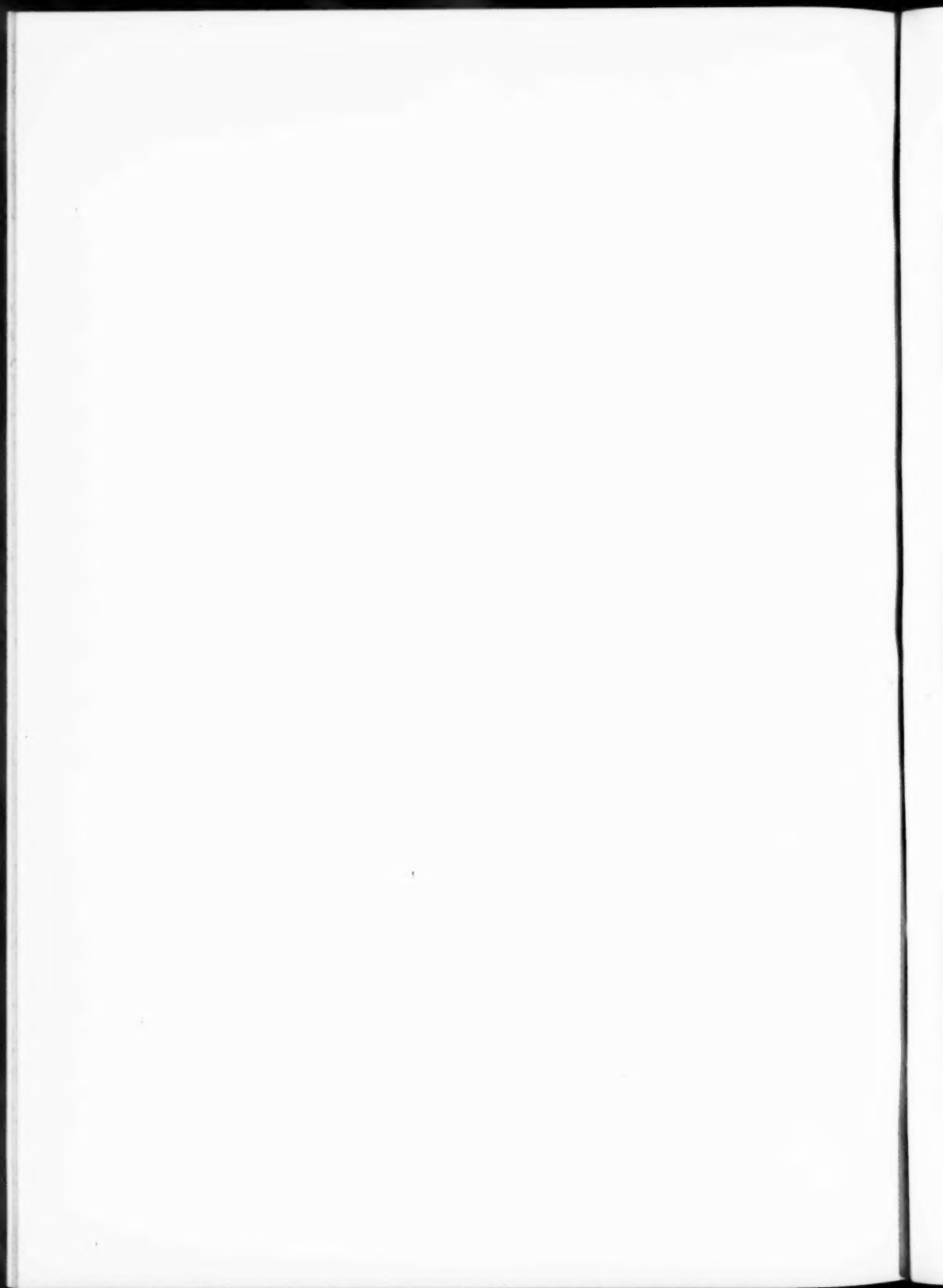
1

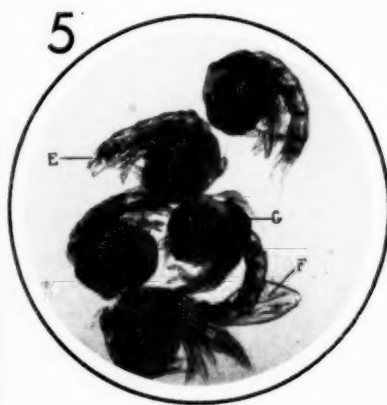
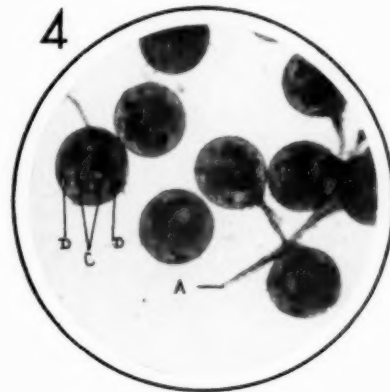
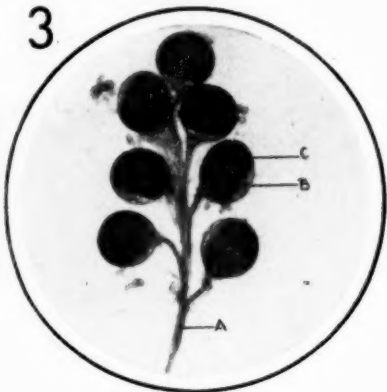
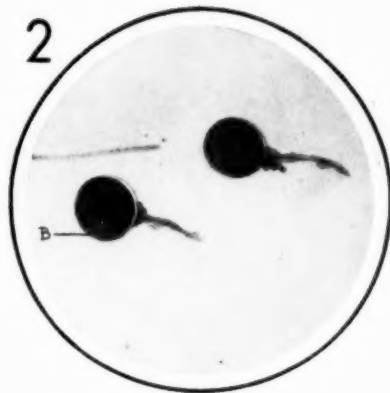
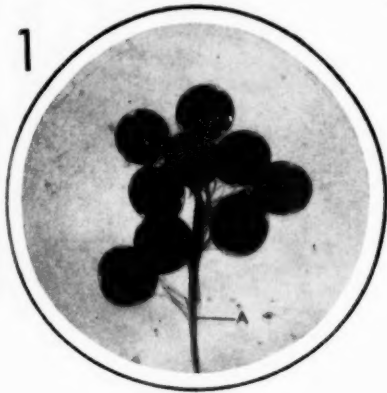


2



3





FACTORIAL ANALYSIS AND SCHOOL SUBJECTS:
A CRITICISM.

(*A Paper from the University of Cape Town*).

By H. A. REYBURN and J. G. TAYLOR.

(Read August 21, 1940.)

In a recent number of the *British Journal of Educational Psychology* there appeared an interesting and important article by Cyril Burt, entitled "The Relations of Educational Abilities." * If the view advanced there of the common factors underlying school subjects is sound, it is of great value both to the psychologist and to the practical teacher; and on account of the weight deservedly attaching to Burt's name a close examination of his results seems desirable.

The article referred to is not Burt's first answer to the main problem with which it deals. It is in fact the continuation of work begun in 1909 and discussed in various publications since that time. Nor is Burt's the only analysis of this kind of material. In the same Journal in 1933 there appeared two articles by J. H. Wilson on "Group Factors among Abilities involved in a School Certificate Examination." † In 1935 W. G. Emmett criticised Wilson's results, ‡ but Wilson defended himself, and there is no sign that a further criticism by Godfrey Thomson § did anything to change his views. As some of the considerations relevant to Burt's analysis have also a bearing on that of Wilson and can be exhibited there in simpler form, we propose to include some of Wilson's results in our discussion.

There is one preliminary consideration which governs our entire argument: the point of view from which the whole matter is regarded is primarily psychological and not mathematical. As we see it, a fundamental requirement is that the factors obtained must be objective. This does not mean that they must be concrete processes or that they must be embodied without remainder in any particular test. It merely requires

* *British Journal of Educational Psychology*, ix, p. 45.

† *British Journal of Educational Psychology*, iii, (1) and (2).

‡ Emmett, W. G., "The Tetrad Criterion and Scholastic Examinations," *British Journal of Educational Psychology*, v, (1).

§ Thomson, G. H., "Group Factors in School Subjects," *British Journal of Educational Psychology*, v, (2).

that they should be capable of persisting and maintaining their identity in a variety of contexts, and that they should not be merely relative to a particular battery of tests. They may be mathematical in nature, just as energy is a mathematical concept, but, apart from causal changes, the measure of them in one context must be identical with the measure in another. Suppose, for example, two factors are identified, using test material. Call them g and v . Then, if these factors appear in the classroom situation, they should have the same values as in the tests. That is to say, if a boy is shown by the tests to have a moderate quantity of g and a high degree of v , these quantities should be preserved if the school work is interpreted in terms of these factors. To put it otherwise, if an individual is measured by two sets of tests and the measurements are resolved into factors, the measurements in these latter terms must agree within the limits of random error. Furthermore, when an individual's capacities are interpreted in terms of objective factors, the values given to these factors must not be altered when the tests by which they are measured are augmented by the inclusion of further tests, even although the latter bring fresh common factors into the battery. Suppose we measure a boy by tests involving only g and v as common factors, and we retest with the same tests together with others which also involve m , then the measures of g and v obtained by the original battery and by the augmented battery should agree, allowance of course being made for the reliabilities of the tests themselves.

The postulate that, in the absence of causal changes, the measures of the factors in each individual should remain invariant implies a similar invariance in the factor loadings or saturation coefficients of the tests. That is to say, the contribution of any factor to the variance of a given test must remain the same whatever the constitution of the test battery may be.

There is, however, a limitation to this last statement. Ultimately we are looking for causal factors, but we cannot pass directly to them by means of factor analysis, a point which Burt realises when he insists that factor analysis is concerned with co-variance. Factor analysis in the ordinary sense is only the first step in a longer process. The factor loadings are not direct measures of the extent to which the factors enter into the processes measured: they indicate the extent to which differences in the measurements depend upon differences in the factors—which is not the same thing. A crude example may illustrate the point. Two men differ in the speed and skill with which they can drive a nail into a wall at eye-level. If asked to drive it into the wall at a considerable height, each by means of a ladder may bring the nail to eye-level and perform with his accustomed skill or lack of it. The ladder is essential to the perform-

ance of the task, but it may not appear in the variations with which the task is performed. Examples relevant to school practice are not difficult to find. When an ability has been brought to maximum efficiency, variations of practice beyond this have no effect, and thus practice would not appear as a factor in the results. Nevertheless, it is fundamental to the operation. Another example that might be given, particularly with reference to intelligence tests, is variation of age within certain limits.

If an adequately large and unselected population is tested, all the common factors involved may be expected to manifest themselves in their true proportions. But if the population is limited and selected, this result will not be achieved. Some essential factors may not appear at all in the analysis, and others will appear with false loadings.

From a psychological point of view and for the purpose of anyone who has to handle an unrestricted population, these considerations are important, and only if full weight is given to them can the factors reached be described as completely objective. But for many practical purposes objectivity need not be interpreted so strictly as this. The average schoolmaster deals with a restricted population, selected more or less steadily from year to year in the same way; and, broadly speaking, it is enough for his purposes if the standard of objectivity employed is not that of the unselected population but of the more or less uniformly selected one with which he has to deal. In an analysis made from his point of view certain of the factors may not appear at all, but for him this is unimportant as they are uniformly and adequately effective. Other factors will affect his results in ratios different from those which would be obtained in the unselected population, but again this need hardly disturb him, for he is concerned only with the relative importance of these factors in his own group.

The conclusions which Burt draws from the fact that we are dealing with co-variance are not identical with those mentioned above. The point on which he lays stress is that the variances of different tests or abilities are not equal to one another, and they should not be regarded as equal in the table of co-variances from which the analysis starts. The point is sound, but in the present state of our knowledge it seems impossible to deal with it. A measurement of variance such as Burt desires would require measurement in an unrestricted population in terms of an absolute unit, and such a unit cannot be obtained unless we know the height of the mean above absolute zero. This information in general is unobtainable at present, except in the doubtful case of mental age, and lacking it we cannot obtain objectivity in the fullest sense. The real factor loads can be had only when the variances of the different tests are given their true relative values, but a limited and still useful objectivity is within our

grasp if in the given population we always give the same value to the variance of each test. Such a value must be arbitrary, and the simplest solution is to make the variance of each test equal to unity. This is achieved by using a correlation table as the basis of our analysis.

One further point may be made here. The difficulty of determining the true relative variances of the tests does not affect the proportions in which the variance of any one of them is to be attributed to common and specific factors. If the communality of a test in a correlation table is .5, then 50 per cent. of the variance is due to common factors and 50 per cent. to specific factors, and the ratio will remain the same if the variance is doubled or changed in any other way.

In his article on "The Relations of Educational Abilities" Burt distinguishes between general and group methods of analysis, and he analyses his data by means of procedures drawn from both classes. We propose to consider the results he obtained, and may begin with the general methods.

Burt discusses two general methods which differ in some respects from one another, but which at the same time have certain fundamental features in common. They may be called the least squares method and the summation method, the latter being virtually identical with Thurstone's centroid method.

(1) In both methods the n tests can be regarded as the terminal points of a set of vectors drawn from a common origin in an r -dimensional space, and the first task is to lay down r mutually rectangular axes along which the projections of the n vectors are measured.

(2) The first axis is that which provides the best fit to the vector system as a whole. In the one case this is determined by a least squares method, in the other by drawing the axis through the centre of gravity of the system. When this axis is discovered and the projections on it measured, the dimension which it represents is eliminated and a second axis is drawn in a similar fashion.

(3) The procedure is continued and results in a series of axes such that the projections of the vectors on them are of diminishing importance both the sum of the projections and the sum of the squares of the projections tend to diminish from one axis to the next.

(4) The number of axes, r , laid down in this fashion is limited in both cases by the size of the probable errors to which the entries in the correlation table are subject.

(5) Finally, in both methods the projections on all axes after the first must include approximately equal numbers of positive and negative values, and the only axis on which all the projections can be positive is the first.

We are not concerned here with the differences between the two methods, for, however important they may be in theory, in practice, in the present instance at least, they are negligible. What is of importance is that Burt accepts the mathematical analysis as it stands and identifies these axes with factors to which a psychological significance can be given. Of the two methods mentioned he prefers that based on least squares, and for convenience we reproduce in Table I (A) the saturation coefficients of the factors to which it leads him. The subject-matter of the tests is adequately described in his article and need not be discussed here.

TABLE I.
Burt's Saturation Coefficients.

Test.	A.				B.				C.			
	<i>g.</i>	<i>v.</i>	<i>m.</i>	<i>a.</i>	<i>g.</i>	<i>v.</i>	<i>m.</i>	<i>a.</i>	<i>g.</i>	<i>v.</i>	<i>m.</i>	<i>a.</i>
Composition	862	384	-266	-045	600	725	656	701	-144	095
Reading (comprehension)	685	349	-014	-064	473	675	518	571	-018	-048
Reading (speed)	470	066	020	-033	432	222	401	262	065	017
Dictation	591	330	135	-010	412	532	442	501	048	-096
History	712	043	-172	-121	664	281	615	373	018	102
Geography	688	025	-019	-132	674	241	605	336	107	026
Science	473	375	259	350	284	440	298	469	031	006
Arithmetic (problems) .	737	-337	-284	211	769	530	692	116	053	462
Arithmetic (rules) . .	397	-384	-331	139	364	530	413	-070	001	514
Handwork	579	-333	343	116	595	..	395	..	582	-092	384	091
Drawing	568	-564	075	-123	559	..	372	..	641	-159	352	166
Writing (quality) . . .	492	-158	480	-008	487	..	429	..	481	067	401	-110
Writing (speed) . . .	276	-047	134	-354	281	..	134	..	288	080	183	-198

Notes.—(1) Decimal points are omitted, and two misprints have been corrected.

(2) Matrix A gives the results of the least squares method, Matrix B of the group factor method, and Matrix C is a transformation of A.

(3) The column headings are the factors: *g* standing for General, *v* for Verbal, *m* for Manual, and *a* for Arithmetical.

The main criticism which we wish to urge against Burt's position here is that there is no guarantee that the factors obtained in this way have any resemblance to the objective factors for which we are looking. There is nothing in nature to suggest that the largest common factor in any battery of tests is the only one that can be positive, that the other factors should all be bi-polar, and that they should be arranged in diminishing order of importance. This criticism must not be misunderstood. If the data are sufficient for the purpose of the analysis—that is to say, if the analysis can be carried to the correct number of dimensions without being confused by random error—the set of axes obtained in this way is

as a whole equivalent to the set which represents the objective factors, and the two sets of axes define the same vector system. But although the axes as a whole are equivalent to the objective factors, it does not follow that the individual axes have any psychological significance, still less that they are objective in the sense defined above. Nevertheless, on account of the equivalence of the two systems, the axes representing objective factors may be reached by rotating in the common factor space the axes obtained directly by the mathematical analysis. Hence in general, after the latter are obtained, it is necessary to rotate them from their initial positions to other positions where they have psychological significance.

Burt apparently disagrees with this contention, and in particular he holds that when the rotated factors can be regarded as objective, the unrotated factors can also be interpreted as they stand. As Burt puts it in a letter to the authors, "bi-polar factors, without any further rotation, have a psychological meaning whenever the rotated factors also have a psychological meaning." Assuming a case where all the factors, taken objectively in our sense, are positive, the first being general and the others group factors, Burt argues as follows. When a general method of analysis is used, "an average amount of each group ability will be transferred to the first or 'general' factor. The second and later factors will only express deviations from that average. Thus the child who is specifically of a verbal type (say) will be indicated by a plus measurement for the verbal factor, while the child who is of a non-verbal type will now be indicated, not by a zero but by a minus measurement. Each of the secondary factors, therefore, will now be bi-polar, *i.e.* will have negative as well as positive saturation coefficients." *

This contention seems to us to be unjustified. Burt appears to assume that the first factor extracted contains the whole of the general factor together with an average amount of each of the others. This is doubtful. The first axis passes through the average of the whole system and it does not represent the whole of the first factor. It is influenced in its position, and therefore in its character, by every one of the objective factors in proportion to their weights—that is, in proportion to the extent to which they contribute to the co-variance. When this dimension is eliminated and the second axis laid down, the same thing holds. The second axis does not represent the second objective factor measured from a new point, as Burt seems to think; its position is determined by all that remains in the table—that is, by fragments of all the objective factors, including the first, in accordance with their remaining weights. And what is true of the second axis is true of all the subsequent ones, each representing a

* *The Relations of Educational Abilities*, p. 59.

mixture of all the objective factors. It is only by accident that any axis can appear to give a set of measurements which can plausibly be interpreted as representing an objective group factor.*

The argument can be put in another way. If Burt's contention were sound, the objective factors could be recovered by a very simple process. The first factor (general) should be plotted with the second (verbal) and the axes rotated until the negative values are just removed. The new first factor should then be plotted against the third (manual) and the process repeated. Finally, the same treatment should be given to the arithmetical factor. This, if we understand Burt's argument, should remove all the negative loads and give the factors in presumably objective form. But in fact the process is impossible: the average loadings of the first factor decrease with each step, the angles of rotation become larger, and in the end the distribution of the points exceeds 90 degrees. This simple procedure is not adequate to obtain factors with positive loads. To achieve this purpose the second, third, and fourth axes must also be rotated with one another and then again with the first.

This criticism is directed against the particular interpretation which Burt gives to the axes as they are obtained mathematically without rotation, but it can be put in a more general form. The axes are relative to the table from which they are derived, and so also are the projections of the test vectors on them. Consequently, if these axes are interpreted as factors, the factor loadings for each test are dependent on the particular battery used, and in general vary whenever any test is added to or subtracted from it. That is to say, the factors so obtained lack the stability and objectivity which we consider to be essential.

It seems clear therefore that rotation is a necessity, but unfortunately there is no automatic way of doing it. The main weight must be given to psychological probability, and in this connection we have to make use of all the psychological knowledge at our disposal. Two points may be mentioned. In the first place, if the battery includes tests which have been analysed before and of whose factorial composition we are reasonably certain, they can be used to determine the position to which some of the axes at least should be rotated. Secondly, consideration has to be given to the factor pattern as a whole. Other things being equal, preference should be given to an arrangement which makes all the factors significant rather than to one which, while providing meaning for some of them, leaves the others unintelligible. In the long run the latter criterion is the more important, and it enables us to revise and correct identifications

* Burt seems to admit this criticism, and indeed to insist on it, but without drawing the necessary conclusion. See, *e.g.*, the paragraph on pp. 56 and 57 of his article.

made on the basis of inadequate data. But in practice the use of it is subject to considerable difficulty.

A condition of making all the factors intelligible is that we discover the correct number of dimensions, r , and Thurstone has shown that the analysis cannot satisfactorily be carried to this number of dimensions if r exceeds a certain function of n , the number of variables.* If we were dealing with infallible data it would be possible by a process of approximation to determine to any necessary degree of accuracy whether the inequality is satisfied or not. But with fallible material this certainty is not always attainable. Small factors—and they necessarily become smaller as the factorial analysis proceeds—may be obscured by the errors of the correlation table, and in reality more factors may be required than we actually extract. In such a case it is impossible to rotate the axes we obtain to fully significant positions.

If only one dimension is missing, the situation is not without remedy. The increase in the communalities required by this additional factor in general tends to be small, and is of the same order as the error to be expected in their estimation. The additional common factor space is necessary for the rotation of the axes to a position where they all have psychological meaning, but the factor loadings in this additional dimension are on the whole of minor importance, and may often without serious distortion be all put equal to zero.

An artificial example may be introduced here to illustrate the point, and it may also be found useful at a later stage of the argument. Table II shows a factorial matrix for 7 variables and 3 factors, the true

TABLE II.

	i.	ii.	iii.	h^2 .
1	.7	.0	.6	.85
2	.6	.0	.5	.61
3	.5	.2	.3	.38
4	.4	.3	.4	.41
5	.4	.6	.0	.52
6	.5	.6	.0	.61
7	.6	.7	.0	.74

communalities being given in the fourth column. A correlation table was derived from this matrix and analysed by Thurstone's centroid method. The factor loads were calculated to four significant figures,

* Thurstone, L. L., *The Vectors of Mind*, p. 76.

but the cross products were rounded off to two. The loads for the first two centroid factors, and the values of h^2 dependent on these factors, are given in Table III. At this stage all the residuals disappear except

TABLE III.

	i.	ii.	h^2 .
1	.7682	.5070	.847
2	.6530	.4218	.604
3	.6018	.1363	.381
4	.6146	.1108	.390
5	.6146	-.3749	.518
6	.6914	-.3621	.609
7	.7426	-.4345	.740

four, one in the leading diagonal amounting to .02, and three others, .01, -.01, and -.01. The rounding off to two figures has almost completely obliterated the third factor. The average correlation coefficient is .425; and the probable error of this coefficient for 500 cases is .0248. It is clear that if the data had been subject to errors of this order, the true residuals would have been swamped and would have been indiscernible in the complete table. The rounding off of the cross products to two figures is in itself sufficient to destroy the possibility of extracting the small third factor.

The communalities in Table III come very close to the true communalities, and in this respect therefore the centroid analysis into two factors is reasonably adequate. But an additional dimension is required to rotate the axes of the centroid matrix to the position of those of the original factorial matrix; and if an arbitrary one with zero loads instead of the true values is added, a close approximation is obtained.

Unfortunately not all cases are as simple as this. The objective factors lying behind the correlation table may be individually small, but there may be a considerable number of them, so that Thurstone's inequality may not be satisfied. Nevertheless, this may not be revealed by the mathematical analysis. The limit set by the probable errors of the correlation coefficients may stop the extraction of factors at a point where the inequality is still satisfied, whereas in reality several additional factors are required to give the number of dimensions necessary for objective interpretation. When there is reason to suspect that such a situation has arisen the only real remedy is to gather additional experimental data.

If this is impossible, all that can be done is to try to recognise the distorted forms of factors known to be present, and to leave the rest in chaos.

It seems to follow from what has been said that in a new field where factors have not been established there is bound to be at first much groping and fumbling, and any results obtained must be regarded as hypotheses for further trial. Suggestions, however, have been made which, if acceptable, would ease the situation. A restricted type of common factor pattern may be assumed and the analysis thereby facilitated. Burt and Thurstone seem to take this line: Burt's view will be dealt with later, and a reference to Thurstone may be permitted here.

Thurstone assumes as a point of method that a factorial analysis is most satisfactory when it shows "unique simple structure." That is to say, when the axes are orthogonal, (1) each row of the factorial matrix has at least one zero entry, and (2) each column has at least as many zero entries as there are factors. It may not be possible to find such a structure at all, but if it can be obtained it is unique.*

This criterion is a purely mathematical one, and its value for practice depends on the probability that this type of pattern characterises the objective common factors involved in the battery. But how can we know that such a pattern is to be expected? Surely it is only by knowing beforehand with reasonable certainty what the factorial composition of the tests is. That is to say, the discovery of unique simple structure where we have reason to expect it is confirmation of a hypothesis already formed, and logically is neither better nor worse than the verification of any other hypothesis. For example, suppose we find unique simple structure in a set of tests where there is reason to think it is present: the hypothesis is justified. Suppose further that to this battery we now add another test which we have reason to believe involves all the factors, and in a fresh analysis this expectation is also confirmed: the unique structure is now destroyed, but the hypothesis is still justified. The real point, then, is not that unique simple structure or any other mathematical pattern should be obtained, but that a reasonable hypothesis should be verified.

In addition to the difficulty arising from the fact that unique simple structure, if obtainable, is relative to the battery, there is a further danger if the method is generalised. A factor pattern obtained by multiple analysis is not exact, and the true outlines of the factors are obscured by error; hence, if we are allowed to distribute the error as we please, it is possible to find such a structure more often than it really occurs.

Burt's attitude to this problem differs from that of Thurstone. He also entertains the idea of a unique structure, although he gives it a different interpretation. It is common ground that the factors obtained by multiple

* Thurstone, L. L., *The Vectors of Mind*, pp. 155 f.

analysis should, in the first instance at least, be independent; but unfortunately the term independent is ambiguous. Two meanings are relevant here. (1) Two factors may be said to be independent when the measures of them in an unselected population have zero correlation. Applied to a battery of tests and regarded geometrically, this gives us a set of mutually rectangular axes which represent the factors in question. The reference frame is orthogonal, and its orthogonality is a reflection of the statistical independence of the factors in the population. It is in this sense that we use the term orthogonality here, and the condition of it can be stated simply:

$$r_{jk} = a_{j1}a_{k1} + a_{j2}a_{k2} + \dots + a_{jr}a_{kr},$$

or alternatively, the communality, h^2 , of each test is equal to the sum of the squares of the factor loadings of the test.

(2) Burt, however, appears to take orthogonality in a more comprehensive sense, viz. one analogous to and perhaps derived from that which the term has when applied to a matrix. For him the factors are independent when the intercolumnar correlations of the factorial matrix are all zero. That is to say, Burt demands not only that the measures of the factors in the population should be uncorrelated, but also that the factor loads of the variables should be uncorrelated. Using the term in this sense he claims that "if we construct an artificial matrix of correlations from a given set of independent factors, the foregoing method of analysis [*i.e.* the method of least squares] appears to be the only one which will lead back to the factor variances and saturation coefficients as originally given."* The analysis of a correlation matrix into independent factors by Burt's method gives a unique structure which is obtained directly; and this may be the reason why he accepts the factors as they stand without rotation. But uniqueness in this sense, in general, is an obstacle to the search for objectivity. It is entirely relative to the battery of tests, and there is no reason to believe that tests which measure objective factors always arrange themselves in batteries in such a way that their saturation coefficients are uncorrelated. One might even hazard the suggestion that in reality it would be very much more difficult to select a group of tests measuring objective factors and conforming to Burt's conception than it would be to prepare a battery showing Thurstone's unique simple structure. In fact, both conceptions are hypotheses, of uncertain validity, and their relevance to the problem of the analysis of school subjects is not obvious.

* Burt, C., "The Unit Hierarchy and its Properties," *Psychometrika*, iii, 1938, p. 167. This statement is hardly justified as it stands. The condition which Burt states, viz. zero intercolumnar correlation, is necessary but not sufficient for his purpose. In addition, all factors other than the first must be bi-polar and (approximately) centred on zero. This seems a strange and arbitrary interpretation of "independence."

We now turn to the other form of analysis, used by Burt in his early studies, discussed and illustrated in his latest statement on the subject, and employed in principle by Wilson, although in a simpler and perhaps cruder form. Burt calls it the group factor method, and claims that by it also the axes can be placed in their final positions "at a single step." He states that "with correlation tables constructed artificially, this formula (unlike most of those in common use) will lead back to the saturation coefficients from which the artificial table was built up."* The method in its simplest form assumes (a) one general factor running through all the tests, (b) a set of non-overlapping group factors, "each sharply limited to a certain group of variables," and (c) positive factor loadings throughout. In later forms of the method the second assumption is qualified, a moderate amount of overlap is admitted, and technique devised for dealing with it. But these complications need not concern us here, as they are not allowed to alter fundamentally the analysis given either by Wilson or by Burt himself.†

The method as used by Burt begins by deciding which variables contain which group factors, collecting the intercorrelations of all the variables sharing a single group factor into a compact sub-matrix, and arranging the total correlation matrix so that these sub-matrices lie along the leading diagonal. The general factor is then extracted by a method depending on the grouping of the diagonal sub-matrices. If the fundamental assumptions are justified, all the entries in the non-diagonal sub-matrices will vanish, subject of course to variations due to random error, and the diagonal sub-matrices will contain significant entries and will each be of rank one, again subject to the limits imposed by random error.

Wilson's procedure is not so formal, but it is substantially the same. It begins with a factor pattern, extracts a general factor, although not in quite the same manner, and then explains the residuals in terms of non-overlapping group factors. He analyses several correlation matrices, but we shall confine our attention to the first, based on 371 pupils who had completed a normal secondary school course. This number is larger than for the other tables and presumably involves lower probable errors. The variables analysed are seven school subjects, viz. (1) English, (2) History, (3) Geography, (4) French, (5) Algebra, (6) Arithmetic, and (7) Geometry.

Wilson's first problem is to extract the general factor. Unlike Burt, he does this not by a method which employs all the data in the table, but by looking for groups of four variables whose intercorrelations can be

* *The Relations of Educational Abilities*, pp. 65 and 54.

† A method which attempts to deal with these difficulties, based on what is called the B-coefficient, is employed by Holzinger and Harman in an article entitled "Comparison of Two Factorial Analyses" in *Psychometrika*, iii, 1.

attributed to a single common factor. Using the tetrad criterion as a guide, he decides that there are three such groups, each containing History, Geography, and French, and having as the fourth members Algebra, Arithmetic, and Geometry respectively. The saturation coefficients obtained for the three subjects that are common to the three groups are not identical in the three arrangements, but Wilson decides that the discrepancies may be attributed to random error and that it is therefore the same factor which appears in each case. He then assumes that English has no group factor in common with Geography or with any of the mathematical subjects, and on this basis obtains a value for the loading of the general factor on English.

Eliminating the influence of this first factor by a method which implies that all the factors are orthogonal, he decides that three non-overlapping factors are required to explain the residuals. Putting coefficients from the original correlation table on the right-hand side, he obtains a sufficient number of equations to determine the group factor loadings of four of his variables. The loadings of the group factors on the other three variables are not determinate, but he divides the still undistributed portion of the co-variance between the factors in a manner which he does not fully explain. The result of these operations is shown in Table IV. The correlations derived from this table are compared with the correlations of the original table, and the agreement is declared to be satisfactory.

TABLE IV.

Subject.	<i>g.</i>	<i>e.</i>	<i>e.</i>	<i>e.</i>	Specific factor.	<i>h</i> ² .
English . . .	·611	·341	·715	..	0	1·0
History . . .	·686	·728	0	1·0
Geography . .	·756	·655	·571
French . . .	·575	..	·249	..	·779	·393
Algebra . . .	·591	·708	·387	·850
Arithmetic . .	·579	·476	·644	·585
Geometry . . .	·575	·544	·613	·624

As we have already pointed out, the factors obtained by a group method such as this are orthogonal if the assumptions on which it rests are justified. Consequently, within the limits of random error, they should be convertible by means of an orthogonal transformation into the results obtained by a valid general method.

Using the centroid method, we obtained the factors and communalities shown in Table V.

TABLE V.

Subject.	i.	ii.	λ^2 .
English . . .	·6939	·4915	·7231
History . . .	·6850	·4021	·6309
Geography . . .	·6904	·1166	·4902
French . . .	·5860	·1399	·3630
Algebra . . .	·7708	—·4766	·8213
Arithmetic . . .	·6858	—·3061	·5640
Geometry . . .	·7263	—·3477	·6484

That these two factors are all that can be extracted significantly is shown by the fact that the mean residual, taken regardless of sign, is ·017, and the probable error of the average correlation coefficient is ·028. If there are other factors, they are obscured by random error, and their contribution to the communalities can only be of the same order as the error itself.

Comparison of the final columns in Tables IV and V shows that the two analyses are not equivalent; and in considering the reason for this fact, we may draw attention to a characteristic of Wilson's method. In extracting his first factor he applies the tetrad criterion three times to groups of four variables. The correlation table is not used as a whole, and the direction of the first axis is determined only from a restricted portion of the data. Such a procedure is equivalent to surveying a large tract of country from a short base, and when it is adopted angles must be measured with exceptional care and accuracy. This is a weakness which attaches to the method as a whole. But instead of taking special precaution, Wilson has, as Emmett points out, used the tetrad criterion with considerable laxity. He presents the tetrad differences derived from two of his three quartets of tests, together with their probable errors. If these tetrad differences are divided by their probable errors, and the distribution of the quotients compared with a normal distribution in which $\sigma = 1/6745$, the test for goodness of fit gives

$$P = 1.7 \times 10^{-14}.$$

That is to say, the general factor does not fit the data.

To this Wilson would doubtless reply, as he did in effect to Emmett, that when the correlation table is reconstructed from his complete factorial matrix, it corresponds reasonably well to the original data. This is true. We tested the fit and found it highly satisfactory. But the reason is simple. The remaining factors are so chosen that they compensate for the deficiencies of the first one. The residuals due to the first factor are too large: the

residuals due to the other factors are too small—indeed, five of them are zero. The coat has been made too long, but by cutting the trousers too short the maker has come out on the right amount of material. It is sometimes forgotten that a group of residuals may deviate from theoretic expectation by defect as well as by excess; both deviations are equally improbable.

But even if Wilson's factors were orthogonal and were justified by the data, the results of his analysis, although they would be possible, would not be necessary. As Thomson pointed out, the factor pattern adopted by Wilson is only one of an infinite number that would fit the data equally well, and no valid reason is given for preferring it. We have already shown that two common factors could account for the data, and the first question to ask is whether the axes given by the centroid analysis can be rotated into a psychologically significant position. Due trial suggests that this is not likely, and hence it may be agreed that a larger number of factors is probable. The next step is to try three; and it may be remarked that the factors reached by the centroid analysis of Wilson's data bear an interesting resemblance to those shown in Table III, which were really due to the three factors shown in Table II. A similar interpretation might be suggested here. If a column of zeros is added to the centroid matrix (Table V) and the matrix is multiplied by the following orthogonal transformation:—

i.	ii.	iii.
.8041	-.3714	-.4643
.1261	-.6565	-.7437
.5810	-.6565	-.4811

it gives the factor loadings shown in Table VI.

TABLE VI.

Subject.	i.	ii.	iii.
English62	.58	-.04
History60	.52	-.02
Geography57	.33	.23
French49	.31	.17
Algebra56	-.03	.71
Arithmetic51	-.05	.55
Geometry54	-.04	.60

With a little ingenuity a meaning might be found for these factors. On the other hand, a bi-factor interpretation may be preferred, such, for example, as is shown in Table VII, derived orthogonally from the same data.

TABLE VII.

Subject.	i.	ii.	iii.
English42	.73	-.07
History45	.66	-.04
Geography55	.42	.07
French46	.39	.04
Algebra85	-.04	.31
Arithmetic71	.05	.23
Geometry76	.04	.26

Table VII gives a simpler structure than Table VI, and this is an advantage if there is reason to believe that the original data are likely to show such a structure. But in the absence of such information, any one arrangement is as good as any other. Finally, we may remark that it is inadvisable to attempt an analysis into four factors, for with four factors seven variables are not sufficient to determine the communalities, and the vector system itself becomes indeterminate.

We may now return to Burt's treatment. The arrangement of the sub-matrices which his method requires is given on page 50 of his article, and the results which he obtains are shown in Table I (B) above. If the underlying assumptions are justified, then when the intercorrelations due to the general factor are subtracted from the corresponding coefficients in the original correlation table, the residuals in the non-diagonal sub-matrices should vanish, within the limits of random error. This test may be applied. Dividing the residuals in these sub-matrices by the probable error of the average correlation coefficient, we find the probability that these residuals can be explained as the effect of random error to be

$$P = 6.1 \times 10^{-18}.$$

More strictly, each residual should be divided by the probable error of its own coefficient, and that might raise the probability slightly, but, on the other hand, to compensate for this, we have omitted the three largest residuals from the calculation.

The second factor covers the first seven variables and is described by Burt as verbal in nature. Examining the residuals left after the correlation due to the general factor has been subtracted, we find that a single

factor can indeed be held to explain them. Extracting this factor by means of Spearman's formula * and computing the correlations due to it, we may compare the resulting matrix with the diagonal sub-matrix remaining when the general factor is removed. If the error to be expected is assumed to be the probable error of the average original coefficient, the residuals are somewhat too small, and the probability that they are due to chance is approximately .20. On the other hand, when a similar treatment is accorded to the mechanical factor held to underlie the last four tests, the residuals are too large, and the probability that they are due to chance alone is approximately .18. The third group factor is confined to two variables, and consequently little useful can be said about it. In dealing with these sub-matrices we have assumed that the residuals should be of the same order as the probable errors of the original coefficients. There may be reason to suspect that this assumption attributes a higher value to the residuals than they should have. If so, the fit of the verbal factor to the sub-matrix is better than we have represented, but that of the mechanical factor is worse.

Burt recognises that his factor pattern is not altogether satisfactory, although he does not state this as strongly as we should be inclined to do. "The theoretic table," he says, "that can be constructed from the four sets of saturation coefficients . . . fits the original or observed correlations pretty closely. There are, however," he adds, "a few instructive instances in which this artificial reconstruction deviates a little from the original." He then refers to a number of residuals which indicate "specific correlation." These could be interpreted as involving additional factors, and it is obvious that any scheme, however bad, could be rectified by additions of this sort. Burt, however, prefers to say that these cross relations "imply an overlapping of the groups," and he suggests a few modifications to deal with the more outstanding points. But he adds significantly that "once these modifications are admitted into the simple non-overlapping scheme, it is not easy to see where to stop." There is a further point, however, that Burt does not mention. The revision of the groups, and in particular their extension to allow for overlapping, requires also revision of the first or general factor. And if Burt is justified in his fear that a more accurate study, with smaller probable errors, would spread each group factor over all the variables, then the whole essence of the method is destroyed.

We may now compare the results which Burt obtains by the group method with those which he obtains by the method of least squares. As we have already seen, both methods project the variables upon a set of mutually rectangular axes; therefore if the two are equivalent analyses of the same data, it should be possible to pass from one to the other by

* Spearman, C., *The Abilities of Man*, Appendix, Equation 21.

means of an orthogonal transformation. Burt provides a transformation matrix by means of which the factors reached by the general method may be converted into those of the group factor system, the results he obtains being shown in Table I (C); and he regards these results as approximating sufficiently closely to the values given in Table I (B). The transformation, however, is not orthogonal. If T is an orthogonal transformation matrix, then $TT' = I$. But when Burt's transformation matrix is multiplied by its transpose, the result is not the identity matrix but that given in Table VIII.

TABLE VIII.

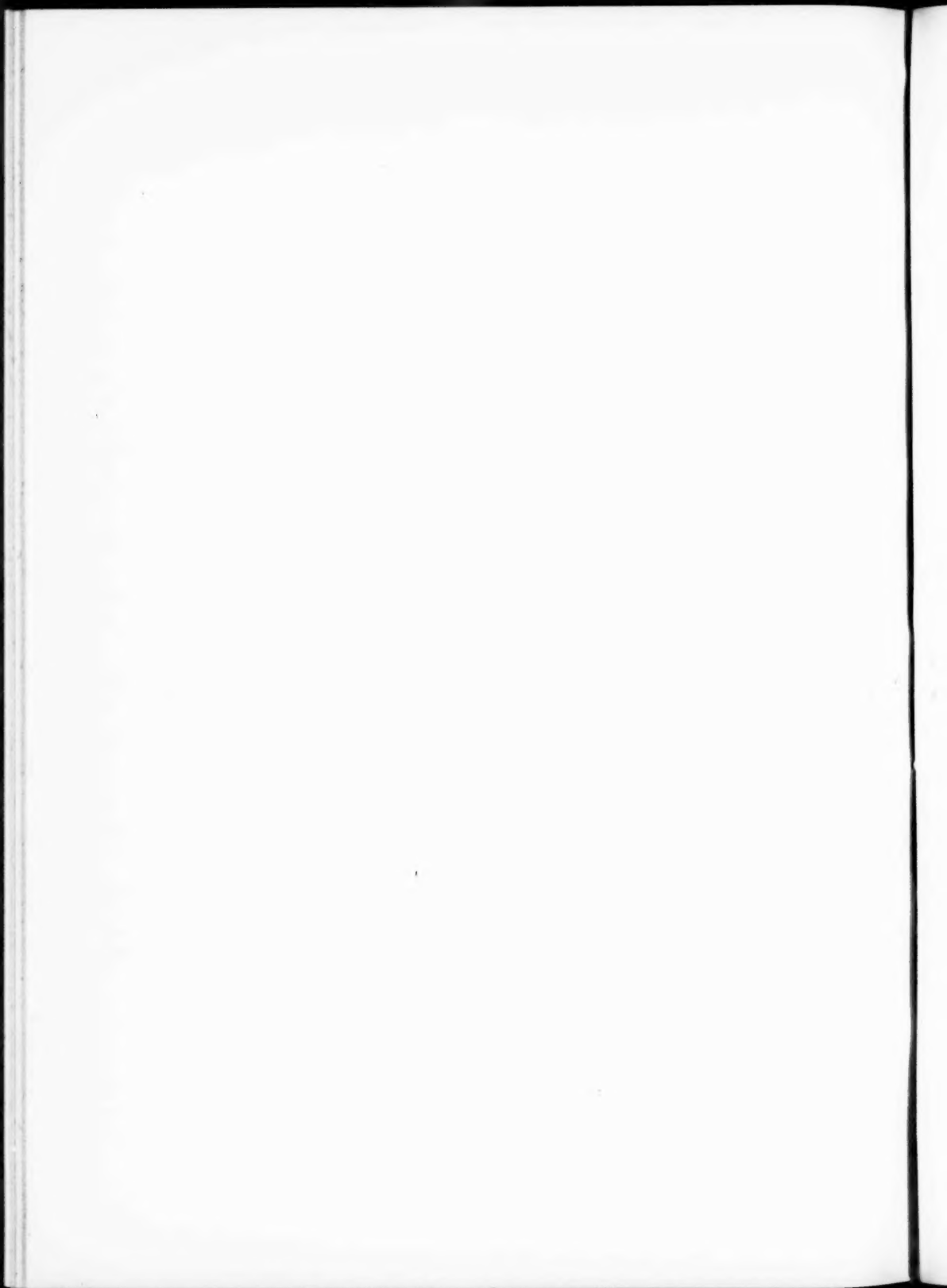
	i.	ii.	iii.	iv.
i.	.823	.225	.252	.136
ii.	.225	.757	-.244	-.138
iii.	.252	-.244	.478	-.190
iv.	.136	-.138	-.190	.639

The non-diagonal entries show that the first axis is inclined towards the other three, and that the latter lean away from one another. The diagonal entries show that each of the axes has been subjected, as Burt recognises, to homogeneous strain. Multiplying the matrix resulting from his general method by this transformation, Burt has obtained a matrix resembling that derived by the group method. But since in the one case the axes along which the measurements are made are orthogonal and unstrained, whereas in the other they are oblique and strained, the very similarity of the matrices is proof that the results which Burt obtains by the two methods are not equivalent. It seems a necessary inference that the assumptions on which the group factor method is based are not justified in the present case.

We confess that, partly in view of these results and partly on general grounds, we doubt whether a satisfactory analysis of the school subjects can be made with the available data. If variables whose factorial composition is clearly known had been included in the battery, it might have been possible to locate some of the axes with reasonable security. The psychological meaning of the remaining axes might then have been fairly easy to discern. As things stand, however, this assistance is lacking, and although in its absence we have tried to rotate the axes reached by general methods to significant positions, we have found none which could be regarded as fully satisfactory. The best result that we obtained gave, firstly, a general factor with not unreasonable loadings; secondly, a bi-polar

factor positively loaded for verbal achievements; and thirdly, a mathematical factor, prominent only in the arithmetic tests and in drawing (which includes geometric drawing). The fourth factor, however, we failed to define. It looks like scraps detached from the first three, together with something which has not yet fully emerged. If another dimension were added to the common factor space, it might be possible to make all the factors significant, but this would probably involve some transformation of the first three factors as well.

The Council desires to acknowledge the receipt of a grant from the University of Cape Town towards the cost of publication of this paper.



THE VASCULAR ANATOMY OF *XENOPUS LAEVIS* (Daudin).

By NAOMI MILLARD, M.Sc.,

Department of Zoology, University of Cape Town.

(Communicated by T. A. STEPHENSON.)

(With twenty Text-figures.)

(Read March 20, 1940.)

CONTENTS.

	PAGE		PAGE
INTRODUCTION	387	RENAL PORTAL SYSTEM	427
MATERIAL AND METHOD	389	DISCUSSION	432
THE ARTERIAL SYSTEM	389	SUMMARY	436
THE VENOUS SYSTEM	410	REFERENCES	438
HEPATIC PORTAL SYSTEM	423		

INTRODUCTION.

A need has long been felt in South African universities for a comprehensive description of the vascular system of *Xenopus*, since this animal is widely used throughout the country for purposes of experiment and demonstration. The muscular system has already been described by Beddard (1895), Grobbelaar (1924 *a*), Noble (1922), and Jones (1933); the nervous system by Paterson (1939); and the skeleton by Ridewood (1897), de Villiers (1924 and 1932), Kotthaus (1933), Paterson (1939) and others. Of the vascular system there exist only a very superficial description by Dreyer (1913 and 1914), and brief accounts by Gilchrist and von Bonde (1922) and Grobbelaar (1924 and 1924 *a*).

Xenopus is the only South African genus of the Aglossa, a group distinguished from the rest of the Amphibia by the absence of a tongue, by an aquatic habitat, and by other anatomical characteristics including the presence of lateral line sense organs in the adult, opisthocelous vertebrae, dilated sacral diapophyses, presence of ribs in the adult, arcifero-firmisternal pectoral girdle, etc. Other members of the group are the neotropical *Pipa* and *Protopipa*, and *Hymenochirus* and *Pseudohymenochirus* of Central Africa.

The distribution of the species of *Xenopus* is as follows:—

Xenopus laevis (Daudin): South and Central Africa, extending as far north as Angola to the west and Abyssinia to the east.

<i>X. mülleri</i> (Peters):	East Africa (Mozambique, Tanganyika Territory, Zanzibar, Kenya Colony, Nyasaland), West Coast (French Equatorial Africa, Benguela), and Belgian Congo.
<i>X. fraseri</i> , Boulenger:	West Africa (French Equatorial Africa, Nigeria, Cameroons, Fernando Po).
<i>X. tropicalis</i> (Gray):	West and Central Africa (Nigeria, Liberia, Belgian Congo).
<i>X. calcaratus</i> , Peters:	Tropical West and Central Africa (Liberia, Nigeria, Cameroons, French Equatorial Africa, Belgian Congo).
<i>X. elvii</i> , Peracca:	North-East Africa (Erythraea and Abyssinia).
<i>X. poweri</i> , Hewitt:	Victoria Falls, Tanganyika Territory.
<i>X. gilli</i> , Rose:	Cape Peninsula.

It has long been recognised that the Aglossa possess on the one hand primitive features, reminiscent of conditions in the Urodeles; and on the other hand highly specialised characteristics, which may resemble those of certain Phaneroglossa, but sometimes have no counterpart among the Anura.

Noble (1922) attempted to reorganise the classification of the Anura on the basis of the modifications of the vertebral column and the thigh musculature. He concluded that the Aglossa form part of one of the more primitive groups of Anura which deviated from the main stem of development at an early stage to take to an aquatic habitat. In response to this new mode of life many specialisations have developed, although certain urodele-like characters are still maintained and betray the primitive origin of the group. *Rana* was not considered by Noble to be a typical example of the Anura, as it is in some ways the most specialised.

The views of Noble are in agreement with those of other authors. Kotthaus (1933), working on the development of the skull, discovered in the first place certain primitive features reminiscent of conditions in Urodeles and fishes, and in the second place a number of secondary characters, some of which might have developed in response to the peculiar method of feeding of the *Xenopus* tadpole.

Green (1931) discussed the pelvic mechanics of the Anura and concluded among other things that "the Aglossa are secondarily readapted to an aquatic life."

Grobbelaar (1924 a), in his work on the muscles and vascular system of *Xenopus*, distinguished a number of primitive characteristics from a number of specialised ones. His conclusions, however, are in direct disagreement with those of Green and other workers, for he maintains

that the presence of epidermal sense organs points to the fact that the Aglossa in the course of their evolution have never left the water. This assumption is probably erroneous.

Escher (1925) described in detail the structure of the lateral line sense-organs in the Anura and claims that these sense-organs are potential to every Anuran at some stage in its life-history, but are only present in the adult in those groups which have returned to the water. He states also that in the structure of these lateral line sense-organs the Aglossa represent a condition intermediate between that of the Urodeles and the larval Phaneroglossa.

It is one object of the present work to determine how far the vascular system conforms to these principles, and whether it throws any light on the phylogenetic history of the group.

MATERIAL AND METHOD.

The results described are based on 48 dissections. All animals were injected with Ranvier's carmine-gelatine mass or Ranvier's Prussian blue through the conus, one of the aortic arches or the abdominal vein. In certain cases, particularly for the veins and arteries of the head, the results of the dissections were verified by means of serial sections from which graphic reconstructions were made. A considerable number of small variations was found from one specimen to the next, and several abnormalities were also encountered. These will be described in a later paper. The nomenclature of Gaupp (1896) was adhered to as far as possible throughout.

ACKNOWLEDGMENT.

The writer wishes to thank Prof. C. G. S. de Villiers and Dr. C. A. du Toit for much helpful advice and for placing at her disposal the library of the Zoology Department, University of Stellenbosch.

The expenses of publication were partly defrayed by a grant from the National Research Council.

The work was carried out in the Zoology Department of the University of Cape Town, and I am indebted to Prof. T. A. Stephenson for reading the manuscript.

THE ARTERIAL SYSTEM (text-fig. 1).

The blood leaves the heart by way of the bulbus cordis and the truncus arteriosus, which divides into two before emerging from the pericardium. Each half gives rise to three arterial arches, namely:

- A. carotis communis.
- A. pulmo-cutanea.
- Aorta.

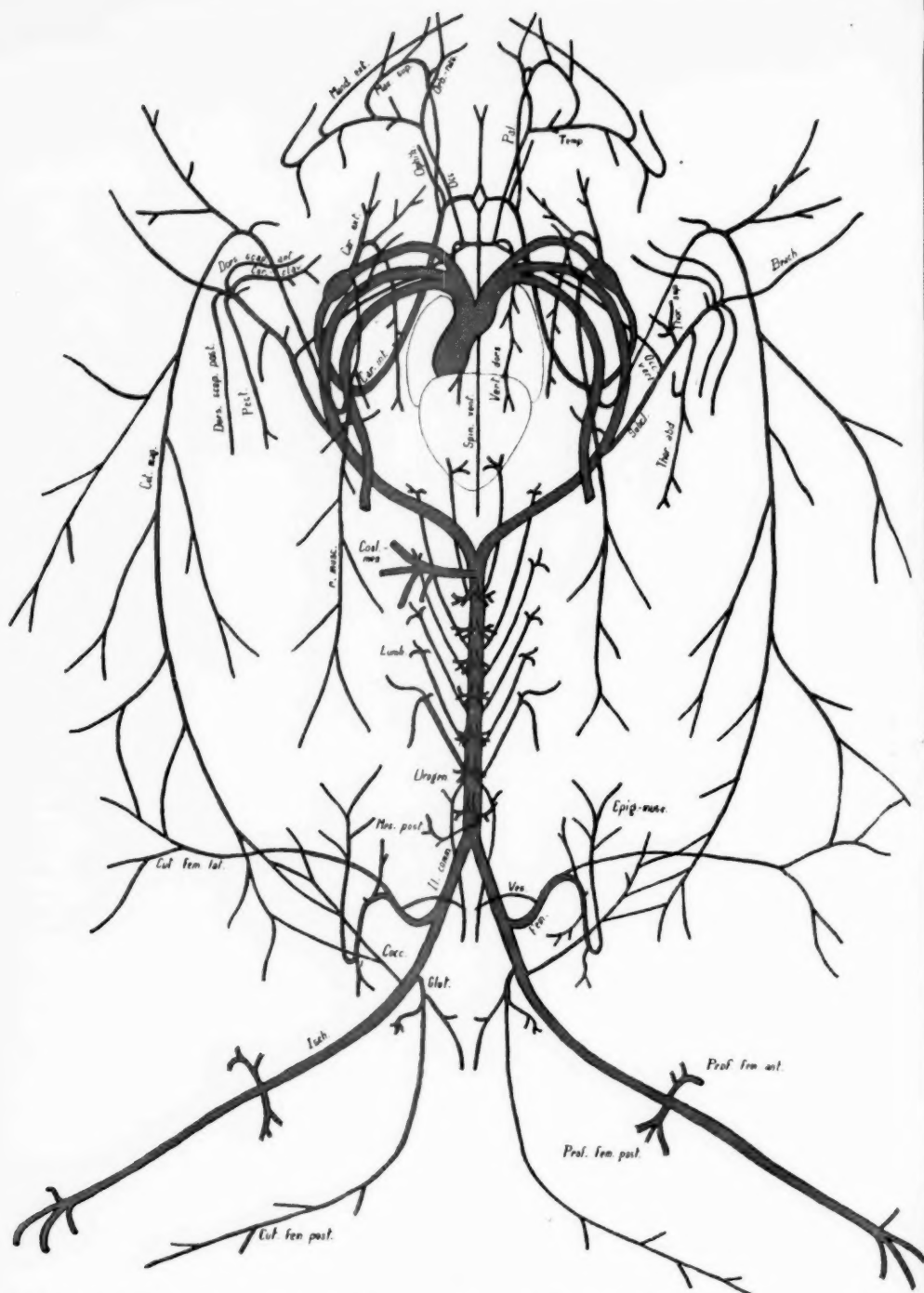


FIG. 1.—A diagrammatic representation of the arterial system of *Xenopus laevis*. Viewed from the ventral surface. For abbreviations see p. 437.

Arteria bulbi cordis.

This artery leaves the left carotid canal of the truncus arteriosus just before the latter divides into two. It passes back over the ventral surface of the truncus and breaks up to supply the bulbus cordis. In *Rana* the A. bulbi cordis emerges from the right carotid canal of the truncus.

Arteria carotis communis (text-fig. 2).

This artery runs forward for a very short distance, and then turns backwards and outwards, lying on the dorsal surface of the *Musculus rectus abdominis*. At the point where it gives rise to the carotid gland two branches are given off simultaneously,* the one running forward (A. carotis externa proper) and the other backward to the muscles of the ventral body wall. The latter is considered to be a ramus muscularis of the A. carotis externa by most authors (e.g. Dreyer, 1913, and Grobbelaar, 1923). Neither in the closely allied *Pipa* nor in *Rana*, however, is there any branch of the A. carotis externa to the ventral body wall. This r. muscularis is thus considered to be a new artery peculiar to *Xenopus*, and it remains for the development to show whether it arises from the A. carotis externa or independently. From the distal end of the carotid gland arises the A. carotis interna.

Ramus muscularis (text-fig. 2).

Runs backwards along the dorsal surface of the *M. rectus abdominis*, sending branches to it and to the *M. sternohyoideus* and *M. transversus*. The details of the small branches vary considerably.

Arteria carotis externa (text-fig. 2).

Divides almost immediately into two; the inner branch divides again, giving three main branches in all: A. laryngea, A. musculo-glandularis, and A. hyoidea.

In identifying these branches the nomenclature of Gaupp was adhered to as far as possible, although the details are very different in *Rana* and in *Xenopus*. According to Gaupp the A. laryngea is not present in *Rana* as a branch of the A. carotis externa, although it may be replaced by another small A. laryngea which is a branch of the aorta. A similar artery, however, is described by Klinckowström (1893) in *Pipa*. The A. musculo-glandularis corresponds to the artery of the same name in *Rana*. The A. hyoidea probably corresponds to the joint stem of the lingual and sublingual arteries of *Rana*, which have become reduced in *Xenopus* because of the loss of the tongue.

* Confirmed by sections.

(a) *A. laryngea*.

Passes dorsally through the hyoid apparatus, between the thyrohyal and the ala, and gives the following branches:—

- i. Forwards to glottis.
- ii. Outwards and upwards to floor of oesophagus.
- iii. Backwards along ventral surface of ala.
- iv. Backwards along thyrohyal and round posterior end of epiphysis.
- v. Several branches to ventral surface of posterior part of oesophagus.
- vi. A very small branch to ventral surface of larynx.

(b) *A. musculo-glandularis*.

Turns inward into the central mass of fatty tissue around the thyroid gland, and runs forward along the ventral surface of the hyoid apparatus.

- i. Backwards along *M. geniohyoideus* (inner part). Small.
- ii. *A. thyroidea*. To thyroid gland and fatty tissue. Double or triple.
- iii. Passes dorsally through hyoglossal foramen and branches up on the floor of the oesophagus. As it passes through the foramen it has been seen to anastomose with the corresponding branch of the other side. May also anastomose with branches of (a) on the oesophagus.
- iv. Forwards along ventral surface of hyoid apparatus, giving small branches to *M. sternohyoideus*, and eventually supplying the anterior cornu on one or both sides.

(c) *A. hyoidea*.

Passes through the attachment of *M. rectus abdominis* and runs forwards along the outer ventral surface of the ala. It gives various branches.

- i. Outwards to fatty tissue on outer edge of ala.
- ii. Forwards to *M. geniohyoideus*.
- iii. Straight forwards.
- iv. This branch may vary somewhat or be absent altogether. It may run forwards and over the edge of the ala on to the floor of the mouth, it may run forwards along the ala to supply the anterior cornu, or it may run outwards past the ala to *M. submaxillaris*.

Arteria carotis interna (text-fig. 3).

Runs backwards along the ventral surface of the ala, turns dorsally over its posterior edge, and runs forwards along the dorsal surface of the oesophagus until it disappears from view in the region of the occipitale laterale. Here it passes along the ventral surface of the skull over a stout membrane connecting the pterygoid to the parasphenoid. In this region it breaks up into its three main branches—*Aa. palatina*, *ophthalmica*, and *carotis cerebralis*. The entry of the *A. carotis cerebralis* into the cranium is difficult to trace by dissection because of the swelling of the *Vena capitis lateralis* in this region. Serial sections through the head, however, show that the artery enters through the base of the foramen prooticum—a large foramen in the lateral wall of the skull which serves for the exit of nerves III, IV, V, VI and *r. palatinus* of VII, and also for the entry of the

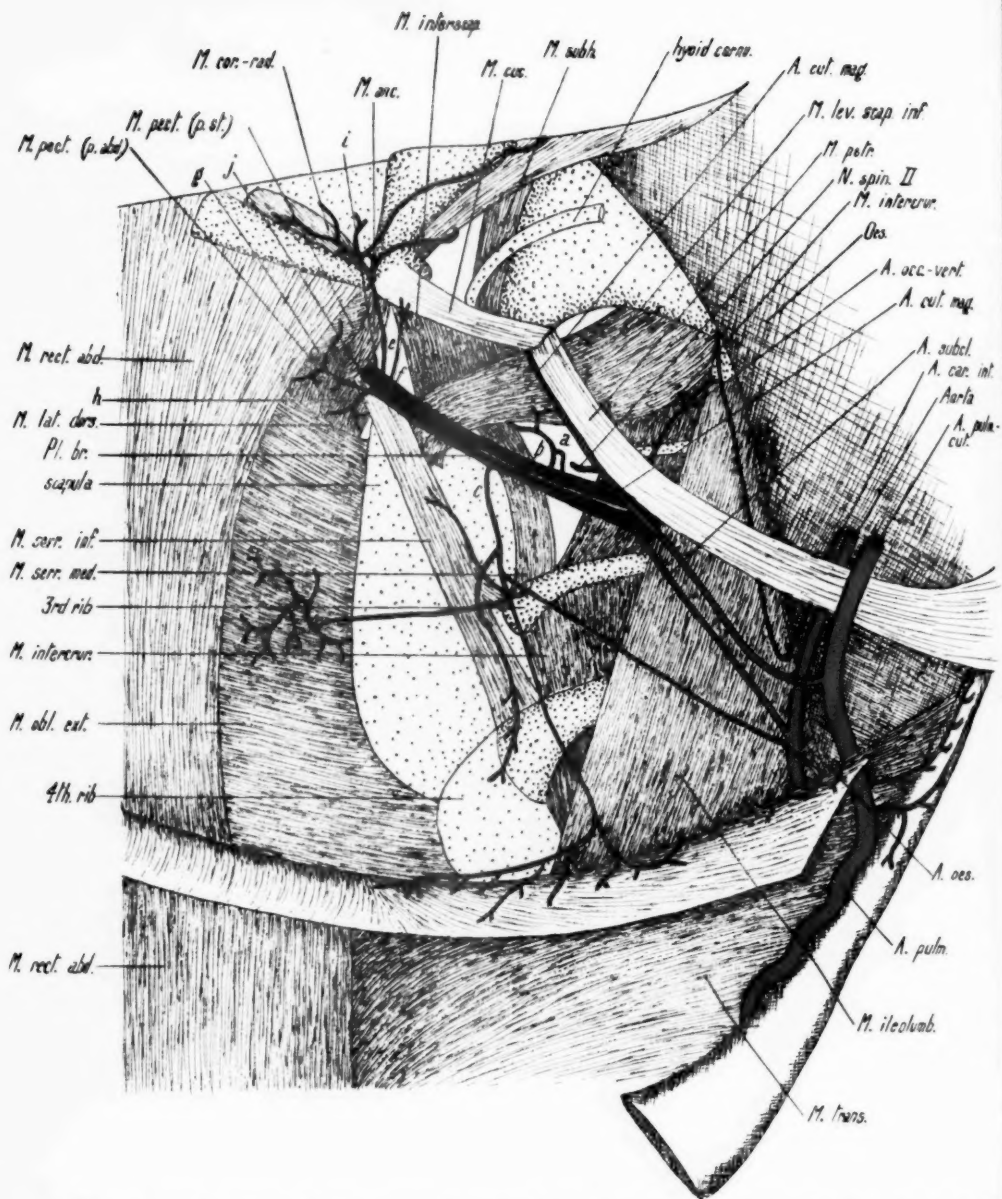


FIG. 3.—A dissection showing the main arteries of the trunk region, particularly the branches of *A. subclavia* (a-j). Ventral view. The heart is removed, the ventral musculature and breast-shoulder apparatus folded to the right, and the oesophagus pulled slightly to the left. For abbreviations see p. 437.

V. capitis lateralis. It does, however, enter independently of all of these through its own membranous foramen. The main branches of the A. carotis interna are as follows:—

(a) *A. palatina*.

Runs forwards along the mucous membrane of the roof of the mouth, giving off numerous small branches. In front of the orbit it divides into two, one branch passing through the outer angle of the orbit and anastomosing with A. maxillaris superior (r. communicans), and the other continuing forwards to the roof of the mouth, with a small branch passing dorsally out of the inner angle of the orbit to anastomose with the r. descendens of the A. orbito-nasalis.

(b) *A. ophthalmica*.

Passes outwards and upwards into the posterior angle of the orbit over the M. levator bulbi, through the eye-muscles, to which it sends small branches, to the bulbus oculi with the optic nerve.

(c) *A. carotis cerebralis*.

Enters the cranium through a membranous aperture in the base of the foramen prooticum. In the cranium it divides into an anterior and a posterior branch. The anterior branch passes forwards over the optic nerve to unite with its fellow on the ventral surface of the cerebral hemispheres. The posterior branch joins its fellow on the ventral surface of the medulla and passes backwards as a median A. spinalis ventralis. Between the first and second vetrebrae the latter anastomoses with a branch of the A. occipito-vertebralis on either side.

Arteria pulmo-cutanea.

Runs outwards and backwards in the same direction as the A. carotis interna, except that it crosses the M. petrohyoideus ventrally. It gives off the A. cutanea magna and dives through the M. transversus to form the A. pulmonalis.

Arteria cutanea magna (text-figs. 3 and 4).

This artery is not nearly so well developed as in *Rana*. It passes outwards with the M. petrohyoideus and dives through to the back of the body between M. cucullaris and M. levator scapulae inferior. Among the Anura it is normal for this artery to be unbranched in this part of its course, but in *Xenopus* many specimens are found to have small branches to the M. petrohyoideus, to the oesophagus or to the larynx, which may vary considerably in their arrangement.

On the dorsal side of the body, after giving off small branches to the lymph and thymus glands, the artery breaks up in the skin of the back and side of the body. A number of small branches pass into M. latissimus dorsi, M. obliquus externus, and M. pectoralis, and in the posterior region several branches anastomose in the region of the lymph hearts with branches of the A. coccygea (branch of A. ischiadica).

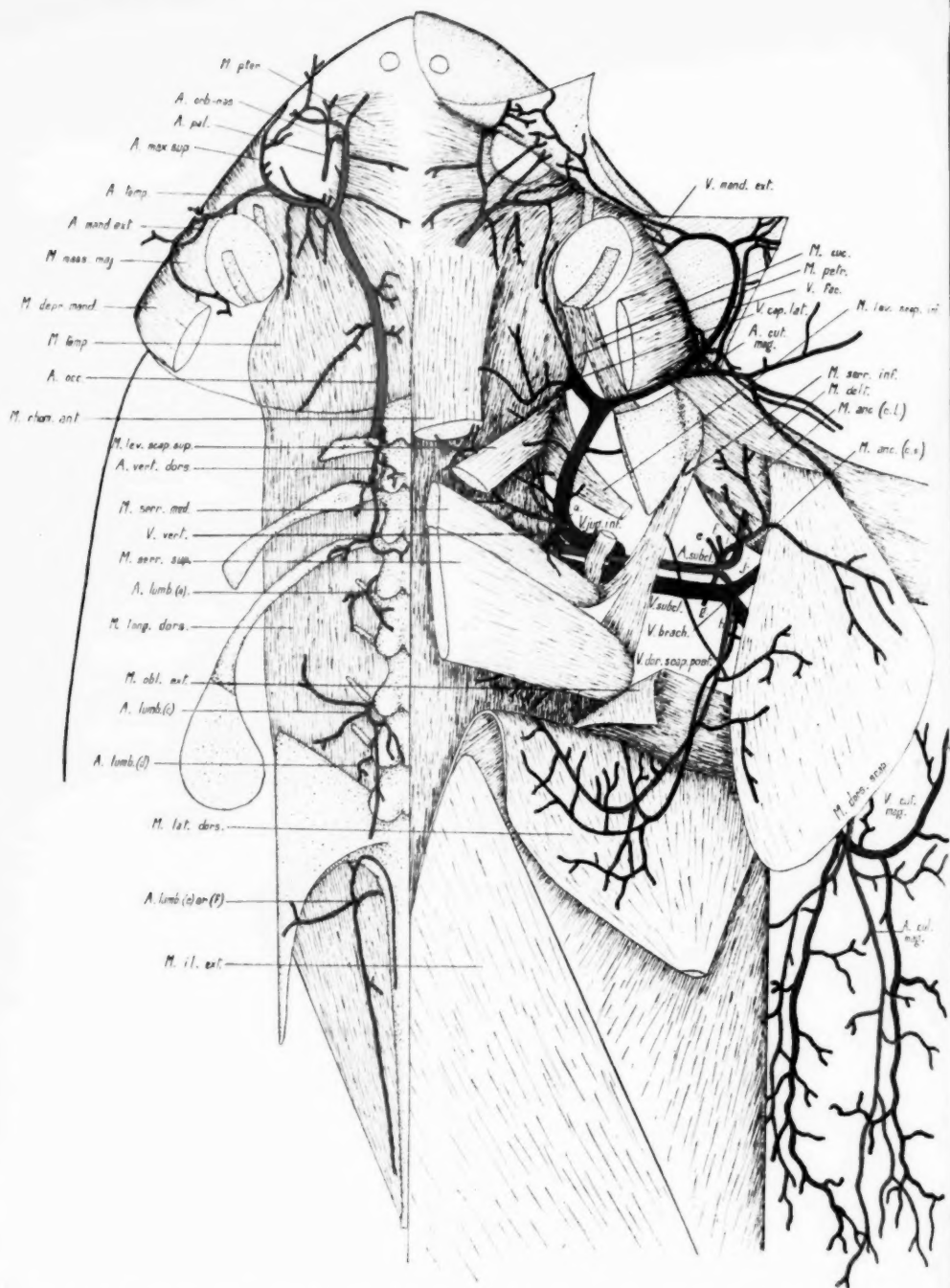


FIG. 4.—A dorsal view of the blood-vessels of the head and trunk. On the right the Mm. dorsalis scapulae and latissimus dorsi are folded back and the scapula partially removed. On the left the scapula and all superficial muscles are removed. For branches of A. subclavia (a-j) see p. 399, and for other abbreviations p. 438.

This artery must correspond to the r. lateralis of *Rana*, but no trace could be found of the other two branches, r. auricularis and r. dorsalis.

Arteria pulmonalis (text-fig. 3).

Runs down the postero-lateral side of the lung, giving one or two small branches to the bronchus and larynx, and eventually dives into the interior of the lung. Inside the lung it consists of one main trunk which gives off small branches along its course, thus differing from *Rana*, where the A. pulmonalis divides into three longitudinal branches inside the lung (Gaupp). This condition was verified by sections.

Aorta.

A. Aorta thoracica (text-fig. 3).

Runs outwards and backwards between the A. carotis interna and A. pulmo-cutanea, and across the dorsal surface of M. petrohyoideus. It passes round to the dorsal side of the oesophagus and gives off the A. oesophagea. The A. laryngea is completely absent in *Xenopus*, but is probably replaced by the laryngeal branch of the A. carotis interna. The A. occipito-vertebralis, instead of coming off the aorta direct as in *Rana*, leaves the A. subclavia about half an inch after its separation from the aorta, and is wrongly named the A. thoracica superior by Grobbelaar. This condition is similar to that found in *Pipa*, where also the A. occipito-vertebralis is a branch of the A. subclavia (A. anonyma, Klinckowström, 1893). Only in one abnormal animal was the A. occipito-vertebralis found to branch off the Aorta.

The A. subclavia leaves the aorta either a little before or a little after the A. oesophagea.

The aorta then passes backwards and inwards, joining its partner in the region of the 8th vertebra to form the Aorta abdominalis.

Arteria oesophagea (text-fig. 3).

A small branch passing inwards to the dorsal and lateral surfaces of the oesophagus.

Arteria subclavia (text-fig. 3).

Runs forwards and outwards across the ventral surface of the M. ileolumbaris on to the ventral surface of the brachial plexus, where it divides into two—the A. occipito-vertebralis and the A. subclavia proper.

Arteria occipito-vertebralis (text-figs. 3 and 4).

Runs forwards and inwards towards the region of the occipitale laterale, where it passes through to the dorsal side of the body close to the first

vertebra. It gives off several branches in this region, including A. vertebralis dorsi (*d*), and continues forwards and dorsalswards as the A. occipitalis. It passes through M. longissimus dorsi and forwards below M. rhomboideus anterior, until it emerges on the dorsal surface of the head just behind the orbit. Here it gives off the A. orbito-nasalis (*e*) and turns outwards behind the eye as the A. temporalis, passes under the zygomatic process of the os tympanicum and breaks up into several branches on the side of the head.

Along its course it gives off small branches to the skin and to M. longissimus dorsi, M. rhomboideus anterior, M. temporalis and M. pterygoideus (the two latter representing A. pterygo-temporalis of *Rana*).

The more important branches are as follows:—

- (a) A small branch just before it passes through to the dorsal side. Branches to supply M. levator scapulae inferior, M. depressor mandibulae, M. intercruralis, and M. ileolumbaris.
- (b) A branch running forwards to supply the vagus ganglion (*r. lateralis*, Gaupp).
- (c) A branch passing into the neural canal between the 1st and 2nd vertebrae. The branches from both sides anastomose with each other in the neural canal and with A. spinalis ventralis of the internal carotid (*r. anastomoticus c. A. basilari*, Gaupp).
- (d) A. vertebralis dorsi. A branch passing backwards dorsal to the ribs and supplying M. longissimus dorsi. Just behind the 4th vertebra it gives a small branch to the skin and disappears. It has never been traced further back than this, and could not be seen to anastomose with the lumbral arteries as in *Rana*.
- (e) A. orbito-nasalis. Runs forwards between the eye and the "os fronto-parietale," giving small branches to M. pterygoideus and to the skin. In the anterior angle of the orbit it gives a branch to the nasal capsule, several to the skin (*rr. frontales*, Gaupp), and one that passes down and anastomoses with the A. palatina of the internal carotid (*r. descendens*, Gaupp).
- (f) A. orbitalis posterior. Leaves A. temporalis just after A. orbito-nasalis and passes outwards and downwards behind the eye.
- (g) A. maxillaris superior. Runs forwards outside the eye, giving off small branches to the skin and surface muscles, and a branch passing inwards and anastomosing with A. palatina of the internal carotid (*r. communicans c. A. palatina*, Gaupp).
- (h) A. mandibularis externa. Passes outwards round the side of the head, over the ventral surface of the lower jaw, and forwards along the inner edge of the latter, giving branches to M. submaxillaris.
- (i) The end-branch of the A. temporalis passes outwards and backwards behind the ear capsule, giving branches to the skin on the ventral side of the head, to the fatty tissue around the thymus, to the M. depressor mandibulae, to the masseter muscles and to the outer surface of the ear capsule. Altogether it represents the A. masseterica plus A. tympanica anterior of Gaupp. (No anastomosis with the A. cutanea magna could be seen, as is present in *Rana*.)

Arteria subclavia (cont.) (text-figs. 3-5).

It follows the course of the Nervus brachialis outwards, giving off several branches along its course and dividing up into 6 end-branches at the point where the N. brachialis dives through the muscles to the arm.

- (a) *A. thoracica superior*. Passes dorsally between nerves I and II, and branches up to supply *M. levator scapulae inferior*, *M. serratus medius*, *M. levator scapulae superior*, *M. serratus superior*, and *M. rhomboideus anterior*.
- (b) Passes dorsally between nerves II and III to *M. serratus superior*. Not always present. Probably represents part of (a).

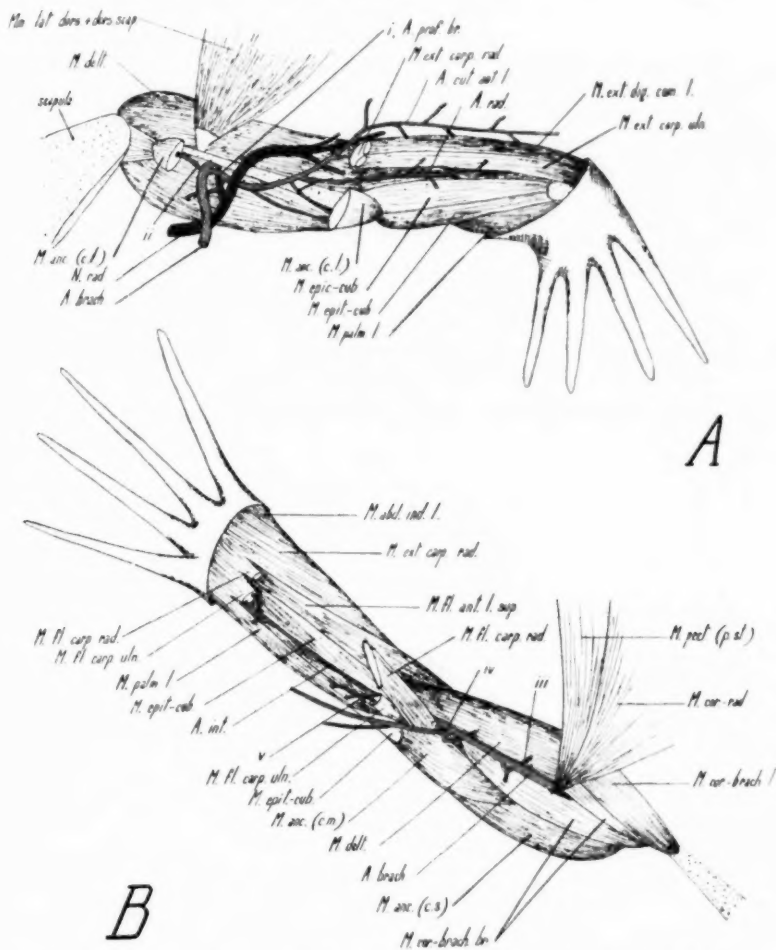


FIG. 5.—The course of the *A. brachialis* in the fore-limb; A, an outer view, and B, an inner view. For branches of *A. brachialis* (i.-v.) see p. 400, and for other abbreviations p. 438.

- (c) *A. thoracica abdominalis*. Branches to supply
- i. *M. transversus*, inner part. Not always present.
 - ii. *M. serratus inferior*.
 - iii. *M. transversus*, outer part.
 - iv. *M. obliquus externus*.
 - v. The 4th rib. Not always present.
- (d) Very rare. To *M. retrohyoideus*.
- (e) *A. coraco-clavicularis*. A ventral branch. Divides into two. One branch passes through to the ventral region of the body between the coracoid and the procoracoid to supply *M. coraco-radialis*, *M. supracoracoideus medius*, *M. mylo-pectori-humeralis*, *M. deltoideus* (inner part), *M. scapulo-humeralis profundus posterior*, *M. pectoralis* (portio sterno-coracoidea).
- The other branch is small and passes through in front of the clavicle to the fatty tissue and skin of the ventral surface, anastomosing on the skin with (g).
- (f) A small branch to *M. cucullaris* and *M. interscapularis*.
- (g) *A. pectoralis*. Passes through to the muscles of the ventral side of the body, supplying *M. pectoralis* (portio sterno-coracoidea), *M. pectoralis* (portio abdominalis), *M. supracoracoideus posticus*, and occasionally *M. obliquus externus*. There is also a branch passing through to the skin of the ventral surface and anastomosing with the *A. cutanea magna*.
- (h) *A. dorsalis scapulae posterior*. Passes dorsalwards and divides into two.
- i. To *M. latissimus dorsi*, *M. obliquus externus*, *M. dorsalis scapulae*, *M. serratus inferior* (small) (r. scapularis, Gaupp).
 - ii. To the skin, anastomosing with (g) (r. cutaneus humeri posterior, Gaupp).
- (i) *A. dorsalis scapulae anterior*. A dorsal branch supplying *M. dorsalis scapulae*, *M. deltoideus* and *M. anconaeus* (caput laterale and caput scapulare).
- (j) *A. brachialis* (text-fig. 5). This is the end-branch of the *A. subclavia*. It enters the fore-limb on the dorsal surface between the caput scapulare and caput laterale of *M. anconaeus*. At this point it gives rise to *A. profunda brachii* and a small muscular branch to *M. anconaeus*, caput laterale. It then passes through posterior to the humerus to emerge on the ventral surface of the arm between *M. deltoideus* and *M. coraco-brachialis brevis*, and passes out to the elbow on the dorsal surface of *N. brachialis longus inferior*. Here it gives a branch to the skin and passes under *M. flexor carpi radialis* and *M. flexor carpi ulnaris* as the *A. interossea*. Along its course the *A. interossea* gives various muscular branches; at the wrist it passes under *M. palmaris longus* and dives into the deeper regions of the wrist to find its way out to the hand. The branches are as follows:—
- i. *A. profunda brachii*. Passes down the arm in close proximity to *N. radialis* beneath *M. anconaeus* (caput laterale) and *M. extensor carpi radialis* and out to the elbow below the attachments of *M. extensor digitorum communis longus* and *M. extensor carpi ulnaris*. In the fore-arm it forms *A. radialis* and runs below and between *M. extensor carpi ulnaris* and *M. epicondylo-cubitalis*. At the wrist it joins the *arcus dorsalis manus*.
- The *A. profunda brachii* gives rise to *A. cutanea antibrachii lateralis* to the skin of the anterior and dorsal arm, and muscular branches to *M. anconaeus*, *M. extensor carpi radialis*, and *M. flexor antibrachii lateralis superficialis*.
- The *A. radialis* gives rise to muscular branches to *M. extensor carpi ulnaris*, *M. epicondylo-cubitalis*, *M. flexor antibrachii lateralis profundus*.
- ii. *A. muscularis* to *M. anconaeus* (caput laterale).

- iii. *A. muscularis* to *M. deltoideus* and *M. coraco-brachialis brevis*.
- iv. *A. cutanea antibrachii medialis superior*. To skin of upper- and fore-arm, with muscular branches to *M. deltoideus*, *M. coraco-brachialis brevis*, and *M. flexor carpi ulnaris*.
- v. *Aa. musculares* from *A. interossea* to *M. palmaris longus*, *M. flexor carpi ulnaris*, *M. epitrochleo-cubitalis*, *M. epicondylo-cubitalis*.

B. Aorta abdominalis (text-fig. 7).

The aorta abdominalis runs posteriorly from the region of the 8th vertebra to a point just anterior to the cloaca, where it divides to form the two *Aa. iliacae communes*. In its course it lies between the kidneys dorsal to the *V. cava posterior*. The *A. coeliaco-mesenterica* is given off from the aorta abdominalis and not from the left aorta thoracica as in *Rana*—a condition which obtains also in *Pipa*. A varying number of urogenital and lumbral arteries are also given off.

Arteria coeliaco-mesenterica (text-fig. 6).

Passes ventrally to supply the gut, liver, gall-bladder, pancreas, and spleen. It divides almost immediately into four main branches.

- (a) *A. gastrica sinistra s. dorsalis*. To dorsal surface of stomach and pancreas.
- (b) Branches into
 - i. *A. intestinalis medialis* to duodenum posterior to the entrance of the bile duct, and to pancreas. Not always present.
 - ii. *A. intestinalis anterior* to duodenum anterior to the entrance of the bile duct. May have a branch to the pancreas.
 - iii. *A. gastrica dextra s. ventralis*. To ventral region of stomach and pancreas.
 - iv. *A. hepatica*. To liver. It has branches to the right, left, and middle lobes, to the gall-bladder (*A. cystica*), and to the pancreas.
- (c) *A. intestinalis posterior*. Divides into two or three long branches to the ilium.
- (d) *A. haemorrhoidalis*. A large branch to the hind end of the ilium and rectum. It gives one or more branches to the spleen (*Aa. lienales*). Sometimes it anastomoses with the *A. mesenterica posterior*.

Arteriae urogenitales (text-fig. 7).

Present much variation. Consist of a number of thick branches leaving the dorsal aorta in the mid-ventral line. These divide up to supply the kidneys, fatty bodies, ovaries and oviducts in the female, and the kidneys, fatty bodies, and testes in the male. The number varies from 6 to 10 in the female and from 7 to 9 in the male. The *A. mesenterica posterior* is given off with the last or second last *A. urogenitalis*.

Arteria mesenterica posterior (text-fig. 7).

Comes off the last or second-last *A. urogenitalis* and branches on the surface of the rectum.

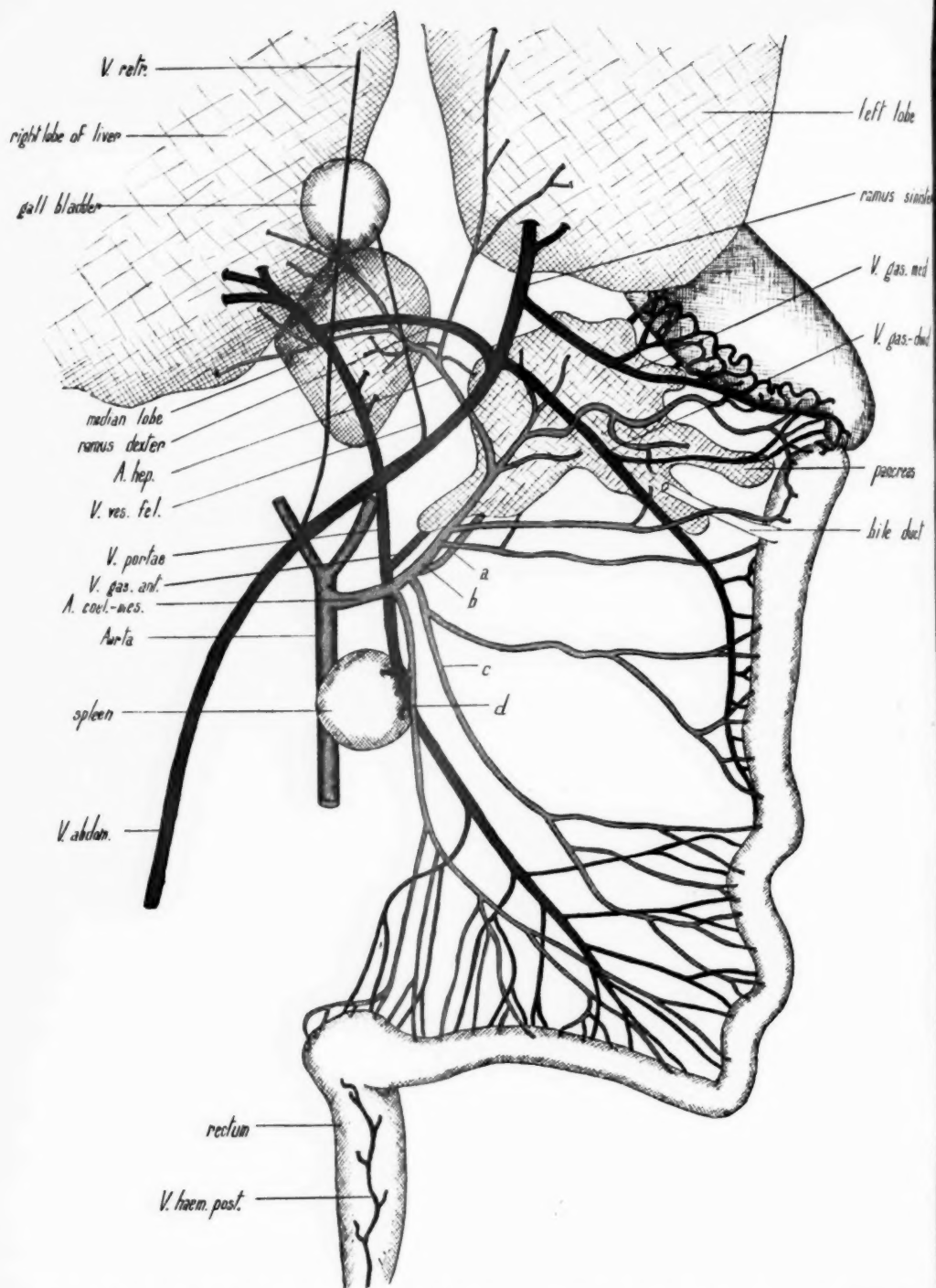


FIG. 6.—A ventral view of the arteries and veins of the alimentary canal. For branches of *A. coeliaco-mesenterica* (a-d) see p. 401, and for other abbreviations p. 438.

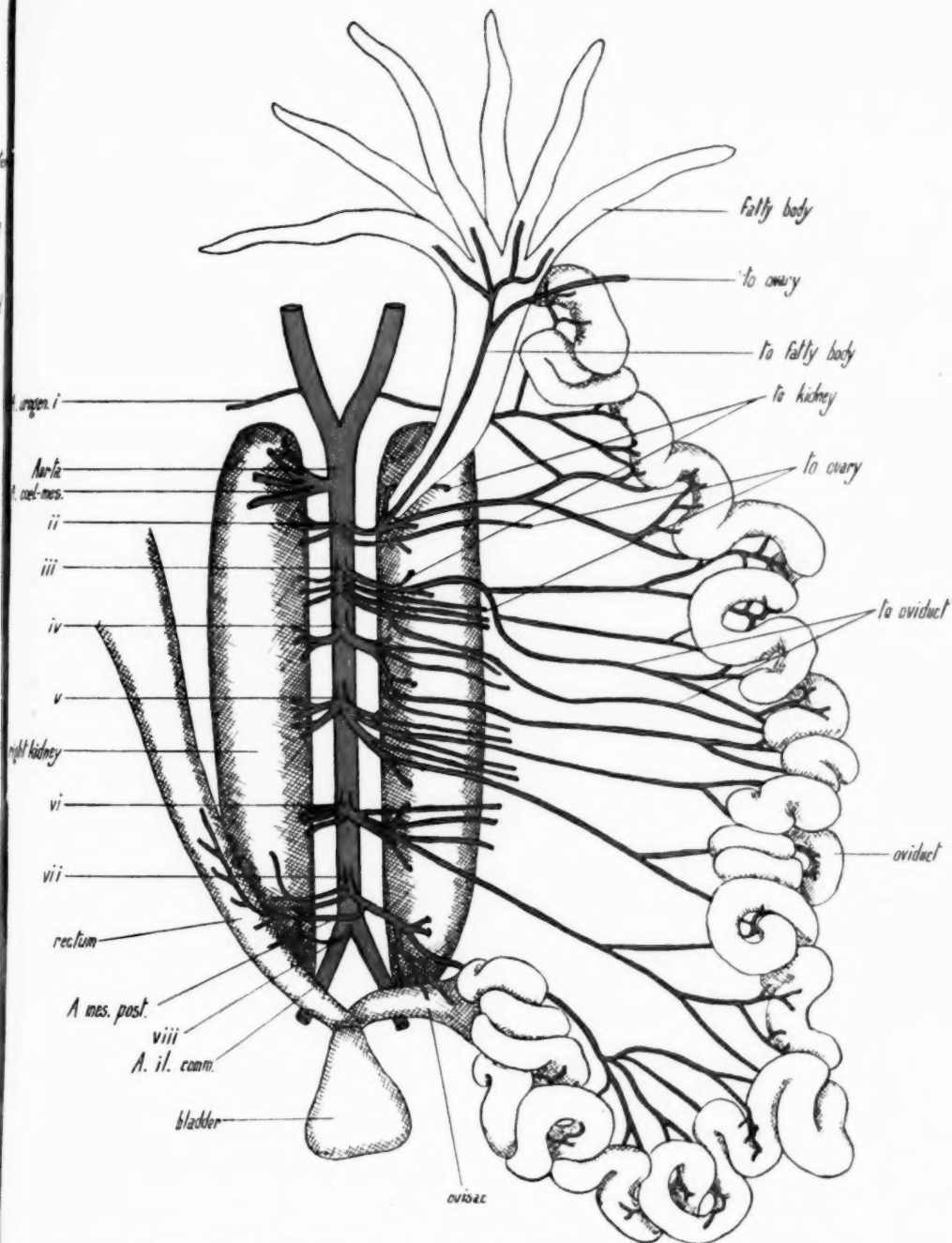


FIG. 7.—A ventral view of the aorta abdominalis and Aa. urogenitales. For abbreviations see p. 437.

Arteriae lumbales (text-fig. 8).

These consist of a number of arteries leaving the aorta either with the Aa. urogenitales or very close to them, and running dorsally and anteriorly to the dorsal body-wall. The full number appears to be 6 pairs (*a-f*), but they are seldom all present, one frog only being seen to possess them all. The six arteries enter the dorsal body-wall behind spinal nerves 4-9 respectively. Their branches vary considerably, but normally each artery gives 3 branches—one to the muscles of the ventral surface of the dorsal body-wall, one through a foramen intervertebrale to the neural canal, and one to the muscles on the dorsal surface of the dorsal body-wall. These latter have never been seen to anastomose with the A. vertebralis dorsi, as is the case in *Rana*. One A. lumbalis (usually *e* or *f*) is generally found to be more strongly developed than the others. The ventral branches supply M. ileolumbaris, M. iliacus externus, and M. coccygeo-iliacus. The dorsal branches supply M. longissimus dorsi, M. iliacus externus, and the skin on the dorsal side of the body.

Arteriae iliace communes (text-fig. 9).

Each runs posteriorly and slightly outwards to give rise to the two main arteries of the leg—A. femoralis and A. ischiadica. The A. vesiculae seminalis (A. uterina posterior lateralis) and the A. epigastrico-vesicalis are absent in *Xenopus* or replaced by branches of the A. femoralis.

Arteria femoralis (text-fig. 9).

Leaves the A. iliaca communis just anterior to the M. iliacus internus, crosses the N. ischiadicus dorsally and the N. cruralis ventrally, and breaks up into a large number of branches to the leg and hind part of the trunk.

- (a) *A. vesicalis* to bladder.
- (b) *A. cutanea femoris lateralis*. Passes out over the ventral surface (or rarely over the dorsal surface) of M. tensor fasciae latae to the skin of the dorsal and lateral sides of the thigh, and anastomoses with the A. cutanea magna.
- (c) Runs forwards along the ilium, crossing the ventral (sometimes dorsal) surface of the tendon of the M. tensor fasciae latae. To M. iliacus externus.
- (d) *A. circumflexa ilium externa*. A strong branch running forwards behind the tendon of M. tensor fasciae latae and M. iliacus externus, and branching deep down to supply M. iliacus externus and its accessory head, M. transversus (occasionally), and M. ileolumbaris. It may be represented by two branches (*r* and *s*) as shown in the diagram.
- (e) *A. muscularis tensoris fasciae latae*. A short branch passing outwards to M. tensor fasciae latae.
- (f) *Aa. musculares iliaceae*. Branches chiefly supplying M. iliacus internus, but also M. iliacus externus. These vary considerably and may consist of one to three branches.
- (g) *A. muscularis* to M. cruralis and sometimes M. iliacus internus.

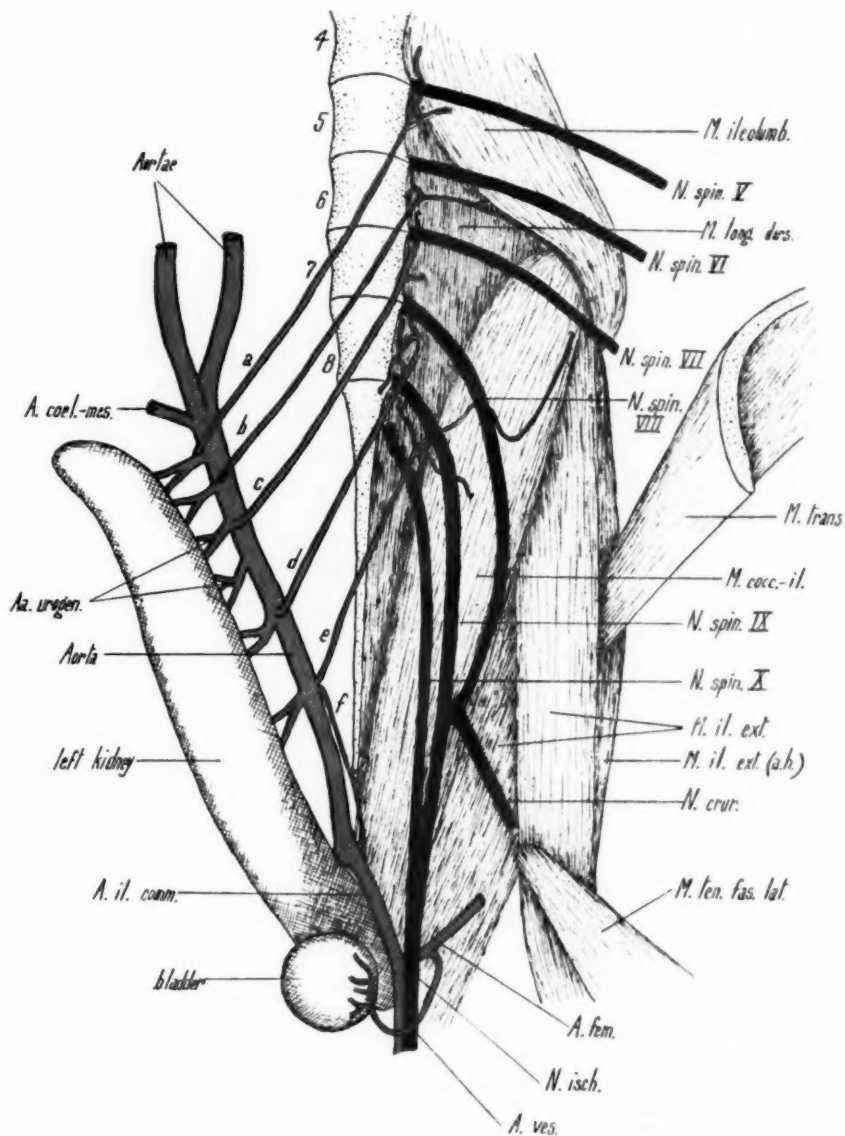


FIG. 8.—The aorta abdominalis and Aa. lumbales, ventral view. The aorta and left kidney are pulled across to the right to show the relations of the Aa. lumbales to the spinal nerves of the left side. For abbreviations see p. 437.

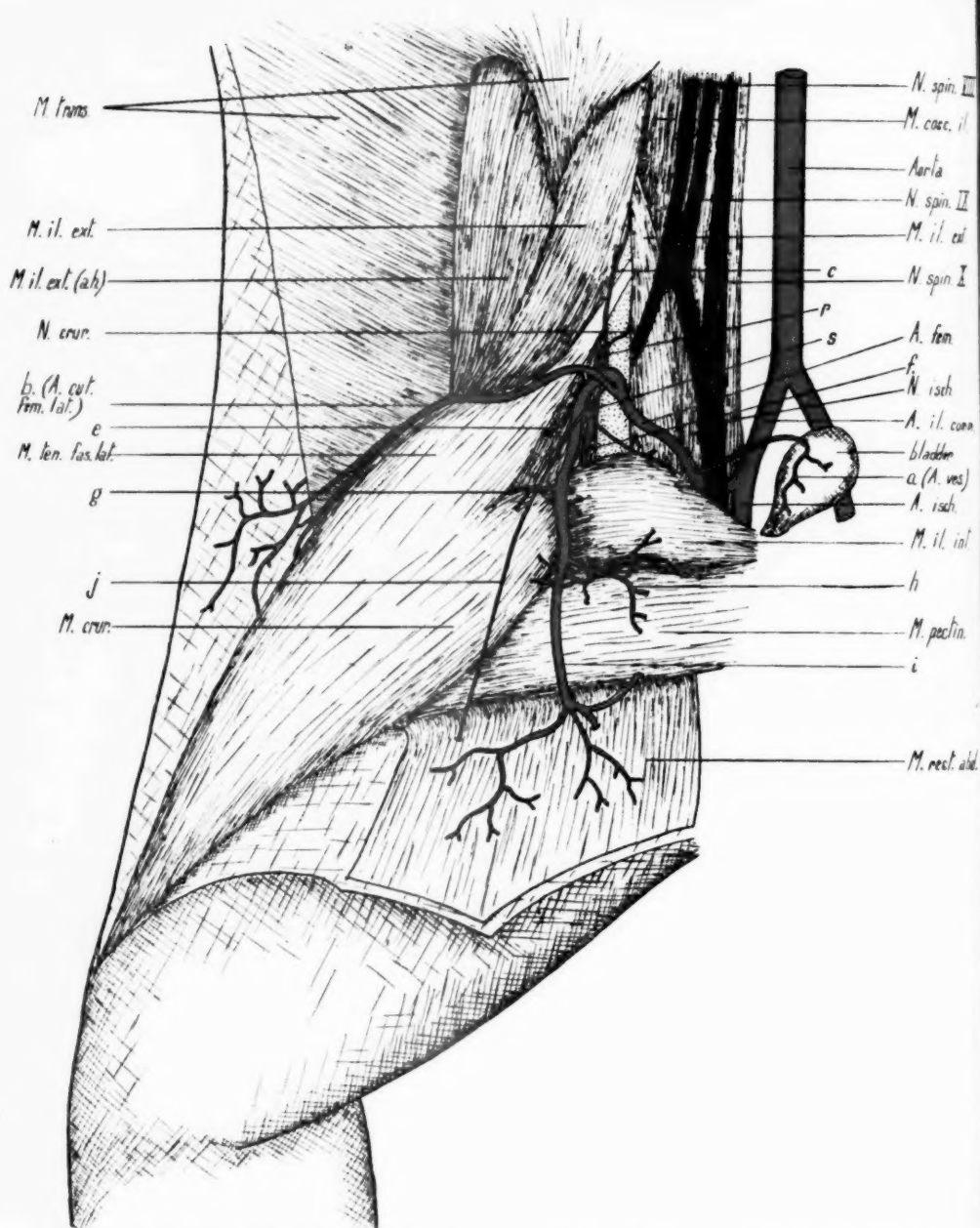


FIG. 9.—Ventral view of the right hind-limb, with the ventral body-wall removed to show the branches of the A. femoralis (a-j), see p. 404. For other abbreviations see p. 438.

- (h) *A. muscularis* to M. iliacus internus, M. pectineus, and M. cruralis.
- (i) *A. epigastrico-muscularis*. This artery takes the place of the *A. epigastrico-communis* of *Rana* in supplying the skin and muscles of the ventral body-wall, but it supplies also several of the leg muscles. Altogether it supplies the skin, M. rectus abdominis, M. obliquus externus, M. sartorio-semitendinosus, M. pectineus, and M. adductor magnus (caput ventrale).
- (j) A branch passing through the posterior edge of M. rectus abdominis to the skin of the ventral surface, with small branches to M. rectus abdominis. Not always present.

Arteria ischiadica (text-fig. 10).

After giving off the *A. femoralis*, the *A. iliaca communis* continues as the *A. ischiadica*. It passes through to the dorsal side of the thigh just ventral to the tendon of M. gluteus magnus. Here it turns outwards into the leg running between M. ileo-fibularis and M. semimembranosus. It gives off four large branches along its course (*a, b, c, d*) and several small ones to M. adductor magnus (caput ventrale) and M. ileo-fibularis.

At the knee the *A. ischiadica* becomes the *A. poplitea*, which immediately gives rise to a large branch, the *A. peronea anterior superior*, and several smaller ones. In the calf the *A. poplitea* is reduced to a very thin vessel running along the tibia below M. tibialis posterior, whereas the *A. peronea anterior superior* is very much enlarged and has apparently taken over the conveyance of the main blood-stream to the foot. The two arteries, however, anastomose in the region of the foot.

Branches of A. ischiadica.

- (a) *A. coccygea*. Arises at the point where the *A. ischiadica* turns outward to the leg, and passes dorsalwards and anteriorly. It gives 2 or 3 branches to the skin of the dorsal surface, which anastomose with branches of *A. cutanea magna*, and small branches to the lymph hearts, M. iliacus externus (accessory head) and M. gluteus magnus.
- (b) *A. glutea*. Leaves *A. ischiadica* opposite *A. coccygea* and runs posteriorly, branching almost immediately into:
 - i. *Aa. pudendae*. There are three *Aa. pudendae*, one to M. compressor cloacae and the posterior part of the rectum, another to the skin in the region of the anus, and a third to M. compressor cloacae.
 - ii. *A. cutanea femoris posterior*. A long artery to the skin of the posterior leg.
 - iii. *A. obturatoria*. A branch to the deeper part of the upper thigh, supplying M. semimembranosus, M. gemellus, M. ileo-femoralis, M. obturator internus, M. quadratus femoris, M. adductor magnus (caput dorsale and ventrale), M. sartorio-semitendinosus, M. obturator externus, M. gluteus magnus.
- (c) *A. profunda femoris posterior*. Comes off the posterior side of *A. ischiadica* about half-way down the thigh and divides up just beneath M. semimembranosus to supply the various muscles.
 - i. *A. muscularis* to M. semimembranosus.
 - ii. *A. muscularis* to M. semimembranosus. More distal than i. Not always present.

- iii. *A. cutanea femoris medialis*. The end-branch of the *A. profunda femoris* posterior, passing through to the skin of the ventral thigh, with branches to the following muscles: *M. gracilis major*, *M. gracilis minor*, *M. sartorio-semi-tendinosus*.
- iv. *A. circumflexa femoris medialis*. Runs slightly forwards and ventrally between *M. adductor magnus* (caput dorsale) and *M. ileo-femoralis*. Supplies *M. adductor magnus* (caput dorsale), *M. obturator externus*, *M. quadratus femoris*, *M. gemellus*, *M. ileo-femoralis*, *M. semimembranosus*.
- (d) *A. profunda femoris anterior*. Comes off the anterior side of *A. ischiadica*, opposite (c), and below *M. ileo-fibularis*. It supplies *M. ileo-fibularis*, *M. cruralis*, *M. glutaeus magnus*, *M. adductor magnus* (caput dorsale and ventrale), *M. ileo-femoralis*, *M. iliacus externus*, *M. iliacus internus*, *M. pectineus*, and *M. obturator externus*. It can be divided into two main branches:
 - i. *A. circumflexa femoris lateralis*, branching up below *M. ileo-fibularis* to muscles of the lateral thigh.
 - ii. *A. circumflexa femoris medialis*, diving down below *M. adductor magnus* (caput dorsale) to the ventral region of the thigh.

Branches of A. poplitea.

- (e) *A. peronea anterior superior*. Passes over the dorsal surface of the knee-joint between the tendons of *M. glutaeus magnus* and *M. ileo-fibularis*, and runs down the dorsal side of the calf just under *M. plantaris longus*.
 - i. *A. muscularis*. Often comes off *A. poplitea*. To *M. glutaeus magnus*, *M. cruralis*, *M. adductor magnus* (caput ventrale), and the knee-joint.
 - ii. *A. suralis communis*. Divides into two to supply *M. plantaris longus* and the skin of the calf (*A. cutanea cruris posterior*). May come off *A. poplitea*.
 - iii. *A. cutanea genu et cruris lateralis superior*. Out to the skin of the knee and calf, with a small branch to *M. glutaeus magnus*.

After this the branches of *A. peronea anterior superior* are irregular and not in agreement with *Rana*. There are branches to the knee-joint, *M. extensor cruris brevis*, *M. peroneus*, *M. tibialis anticus brevis* and *longus*. At the ankle the *A. peronea anterior superior* anastomoses with *A. tibialis posterior* (g) and *A. poplitea*, and also sends out three well-developed branches to the skin.
- (f) *A. circumflexa genu medialis superior*. A small branch to *M. adductor magnus* (caput ventrale and dorsale), *M. gracilis major* and *minor*, *M. semimembranosus*, *M. sartorio-semi-tendinosus*, the knee-joint and the skin of the hind part of the thigh.
- (g) *A. tibialis posterior*. Leaves *A. poplitea* just behind the knee-joint and soon dives into *M. plantaris longus*. It runs down through this muscle, giving branches to it, and at the ankle anastomoses with *A. poplitea* and *A. peronea anterior superior*.
- (h) *A. circumflexa genu medialis inferior*. Passes across the medial side of the tibia and out (next to *M. extensor cruris brevis*) to the skin of the calf and hind part of the thigh. It sends branches also to *M. sartorio-semi-tendinosus*, *M. semimembranosus*, *M. tibialis posterior*, *M. gracilis minor*, and the knee-joint.
- (i) *Aa. musculares* to *M. tibialis posterior*.

THE VENOUS SYSTEM (text-fig. 11).

The arterial blood from the lungs passes into the left auricle by way of the Vena pulmonalis communis. The main blood-stream from the body is poured into the sinus venosus and thence into the right auricle by the two Vv. cavae anteriores from the head and anterior region of the body and the V. cava posterior from the kidneys and liver. It is important to note, however, that this blood-stream is not purely venous, since it receives a certain amount of arterial blood from the various cutaneous veins, the largest of these being the V. cutanea magna. The *renal portal system* conveys the blood from the hind part of the body to the kidneys, and the *hepatic portal system* (in which may be included the V. abdominalis) conveys blood from the gut and ventral body-wall to the liver. The Vv. hepaticae open into the anterior end of the V. cava posterior.

Vena pulmonalis (text-fig. 11).

The V. pulmonalis leaves the lung and runs along the ventral surface of the bronchus dorsal to the liver. Immediately dorsal to the sinus venosus and caudal to the larynx it joins its fellow from the other side to form the V. pulmonalis communis, which enters the left auricle.

Vena cava anterior (text-figs. 12-14).

The V. cava anterior of each side is made up by the junction of the V. subclavia and the V. jugularis interna. The stout vein thus formed passes inwards towards the heart, crossing the three arterial arches ventrally. Immediately next to the heart it receives the thick V. jugularis externa and V. muscularis-thyroidea and opens into the sinus venosus. The V. cava anterior also receives the smaller V. muscularis abdominis.

Vena muscularis abdominis (text-figs. 12 and 13).

A small branch from the muscles of the ventral body-wall. It passes round the lateral edge of M. rectus abdominis (deep portion) and inwards with the V. cava anterior to join the latter usually just opposite the V. muscularis-thyroidea and V. jugularis externa. The point of junction varies considerably, however, and it may join the V. cava anterior opposite the V. jugularis interna, or it may open direct into the sinus venosus. It drains M. sternohyoideus, M. rectus abdominis (deep portion), M. geniohyoideus (sometimes), M. transversus (sometimes), the carotid gland, and the fatty tissue on the lateral edge of the hyoid apparatus.

On the ventral surface of M. sternohyoideus it may anastomose (i) with V. retrosternalis (branch of V. abdominalis) or (ii) with V. epigastrica anterior. This vein is not found in *Rana*.

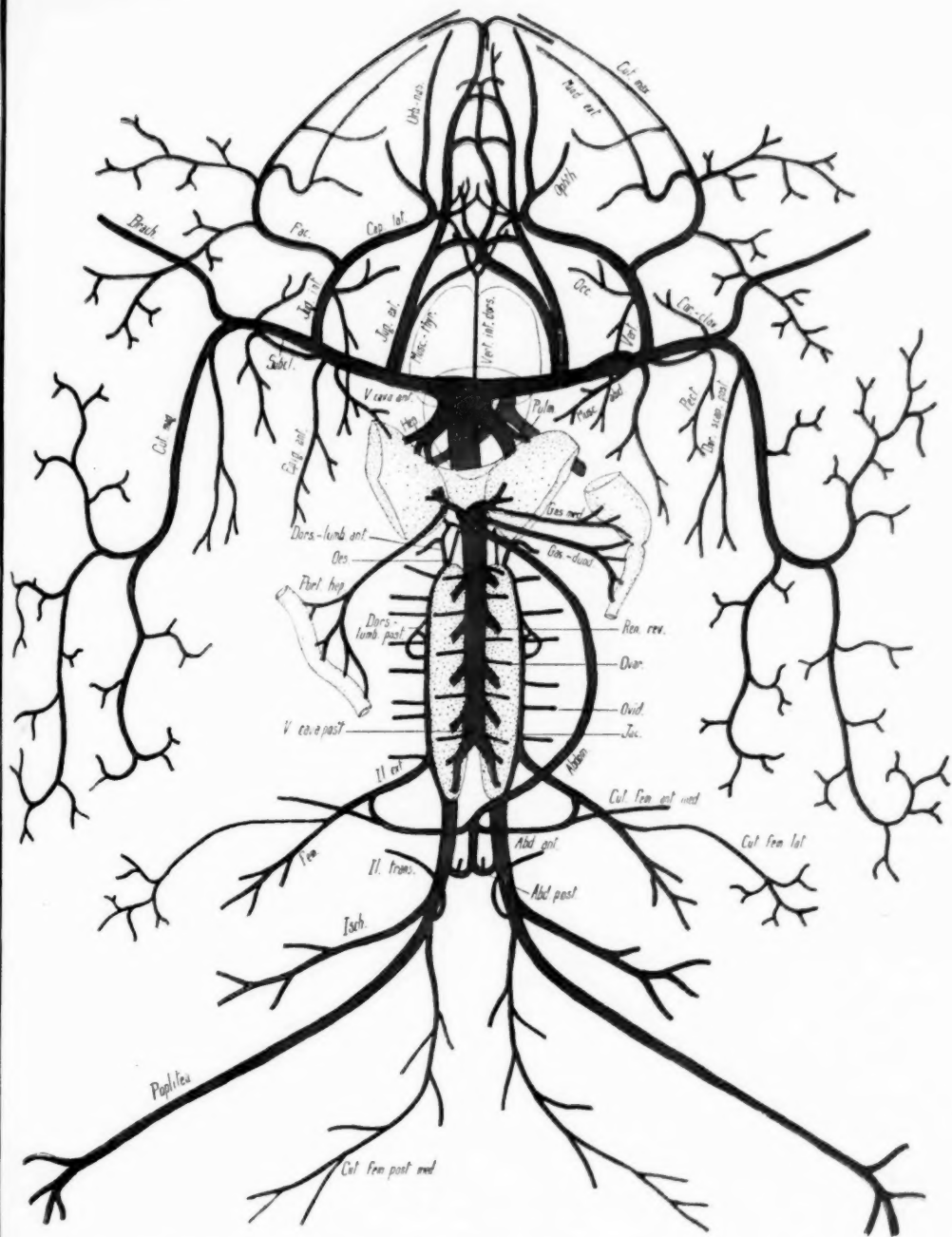


FIG. 11.—A diagrammatic representation of the venous system of *Xenopus laevis*, female. Viewed from the ventral surface. For abbreviations see p. 437.

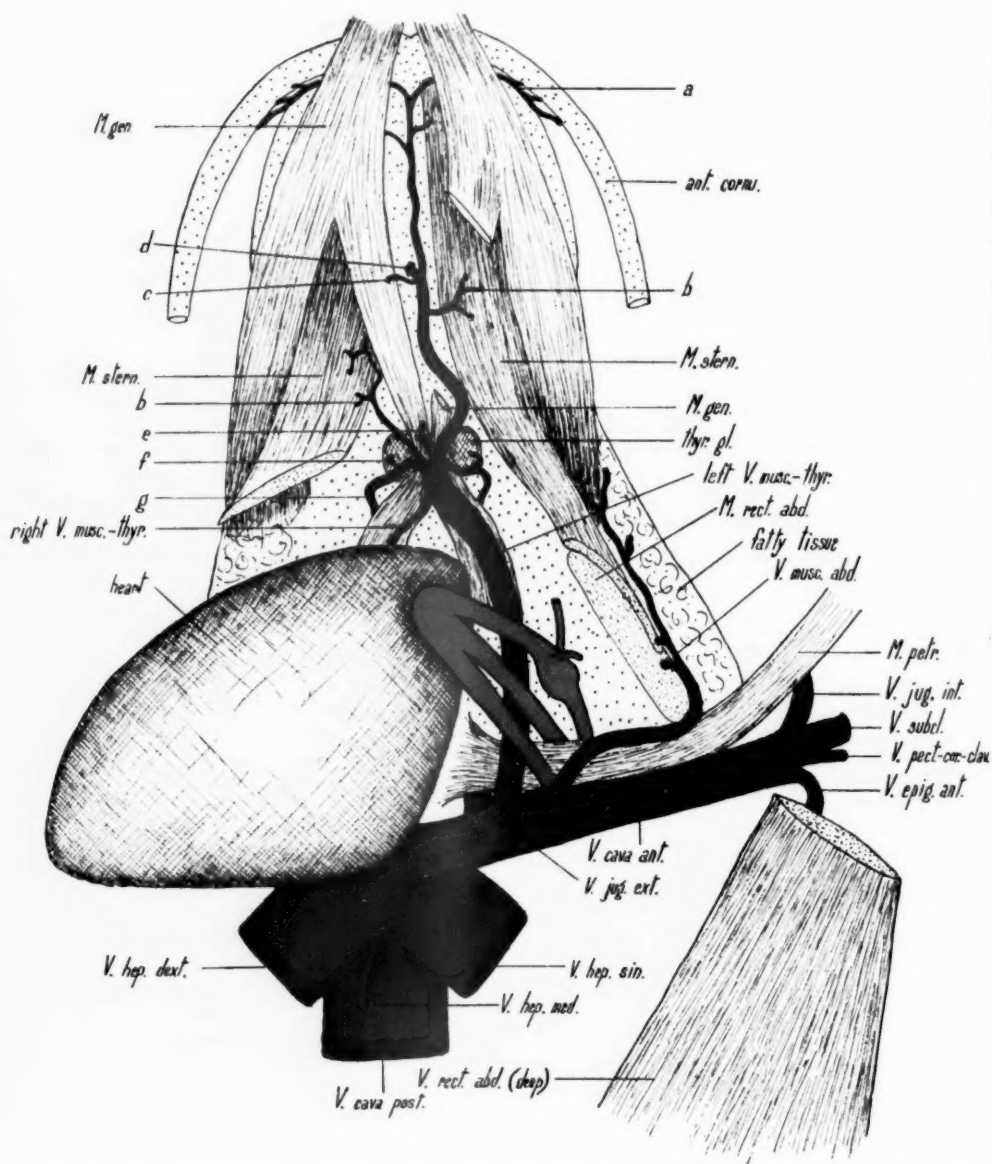


FIG. 12.—A diagram showing the course of the V. cava anterior and the branches of V. muscularis-thyroidea (*a-g*), see p. 413. The dissection is viewed from the ventral surface and the sternum and ventral body muscles are removed. For abbreviations see p. 437.

Vena muscularis-thyroidea (text-figs. 12 and 13).

Commences in the anterior region of the ventral surface of the hyoid cartilage and runs backwards as a single median vein receiving branches from the M. geniohyoideus and M. sternohyoideus and anastomosing with V. jugularis externa through the hyoglossal foramen. It passes ventrally round the right or left side of the inner part of M. geniohyoideus. Here it is joined by a number of other branches from the thyroid gland and surrounding muscles and normally splits into a right and a left half. These branches pass backwards *dorsal* to the arterial arches to join the Vv. cavae anteriores just before they enter the heart.

The two halves are very seldom equally developed. In 69 per cent. of the animals examined the right vein was weaker than the left or absent altogether. In 23 per cent. the left side was weaker or absent altogether, and in only 8 per cent. was there an equal development of the two sides.

This vein is not present in *Rana*.

The branches are as follows:—

- (a) *V. hyoidea inferior*. From ventral surface of both anterior cornua of the hyoid apparatus. Sometimes very poorly developed.
- (b) *Vv. musculares* from M. sternohyoideus.
- (c) *Vv. musculares* from M. geniohyoideus.
- (d) A branch passing through the hyoglossal foramen to anastomose with the V. jugularis externa.
- (e) *V. abdominalis*. A median branch from M. sternohyoideus and M. rectus abdominis (deep part) of the ventral body-wall. This branch may anastomose with the V. retrosternalis (branch of V. abdominalis) on the ventral body-wall.
- (f) *V. thyroidea*. From thyroid gland.
- (g) A branch passing dorsally through the gap between the ala and the thyrohyal to anastomose with the V. jugularis externa. It may leave the V. muscularis-thyroidea before or after the latter divides into two.

Vena jugularis externa (text-fig. 14).

The V. jugularis externa commences in the anterior region of the floor of the mouth, where it receives branches from the mucous membrane of the mouth, the lower jaw, M. submaxillaris and M. geniohyoideus. It runs backwards along the floor of the mouth dorsal to the hyoid apparatus, collecting many branches as it goes. Farther back it leaves the floor of the mouth and runs along the hyoid apparatus between the ala and the thyrohyal to join the V. cava anterior opposite and dorsal to the V. muscularis-thyroidea.

It anastomoses (i) with the V. jugularis externa of the other side on the floor of the mouth anterior to the hyoid apparatus, (ii) with the V. muscularis-thyroidea through the hyoglossal foramen, and (iii) with

the V. muscularis-thyroidea through the gap between the ala and the thyrohyal. These anastomoses are not necessarily always present, although (iii) is almost unfailing.

It is usually found (50 per cent. of the dissections) that the V. jugularis externa of the right side is much better developed than that of the left (in the case of the V. muscularis-thyroidea it is the left side which is usually better developed). In 20 per cent. of the cases examined the left side was better developed, and in 30 per cent. there was an equal development of the two sides.

The branches are as follows (they can hardly be compared with those of *Rana*, as they are so vastly different):—

- (a) *V. mandibularis anterior*. From the anterior region of the lower jaw and floor of the mouth.
- (b) *Vr. musculares* from M. submaxillaris (medial region).
- (c) *Vr. musculares* from the dorsal surface of M. geniohyoideus.
- (d) *Vr. pharyngeae*. A large number of branches from the mucous membrane of the floor of the mouth. Some of these anastomose with branches from the opposite side.
- (e) *V. hyoidea superior*. From the dorsal surface of the right and left anterior cornua, with small branches from the attachments of M. sternohyoideus. It may be absent altogether, in which case the V. hyoidea inferior (of V. muscularis-thyroidea) is well developed.
- (f) An anastomosis with V. muscularis-thyroidea through the hyoglossal foramen. Usually present on one side only.
- (g) *Vr. laryngeae*. These form a network of small veins draining the larynx and are particularly well developed in the male.
- (h) An anastomosis with V. muscularis-thyroidea through the gap between the ala and the thyrohyal.

Vena jugularis interna * (text-figs. 4 and 14).

The V. jugularis interna is a continuation of the V. capitis lateralis, which collects blood from the head and dorsal surface of the body. The latter starts in the region of the foramen prooticum, where it is made up by the junction of the V. ophthalmica, V. orbito-nasalis and the veins from the cranial cavity. It leaves the brain-case with the hyomandibular nerve and runs with it backwards and outwards over the otic capsule, until it emerges from the skull on the posterior surface. Farther back below M. depressor mandibulae it receives V. facialis,† and still farther back V. occipitalis and V. vertebralis. It then turns ventrally as the

* As there is no V. subscapularis in *Xenopus* there is no V. anonyma, since according to Gaupp the latter is formed by the junction of the V. jugularis interna with the V. subscapularis. The work of the V. subscapularis in *Xenopus* is taken over by branches of the V. vertebralis, V. brachialis, and V. cutanea magna.

† In *Rana* the V. facialis passes back over the arm to join the V. cutanea magna.

V. pec
V. epi
Fig.
with

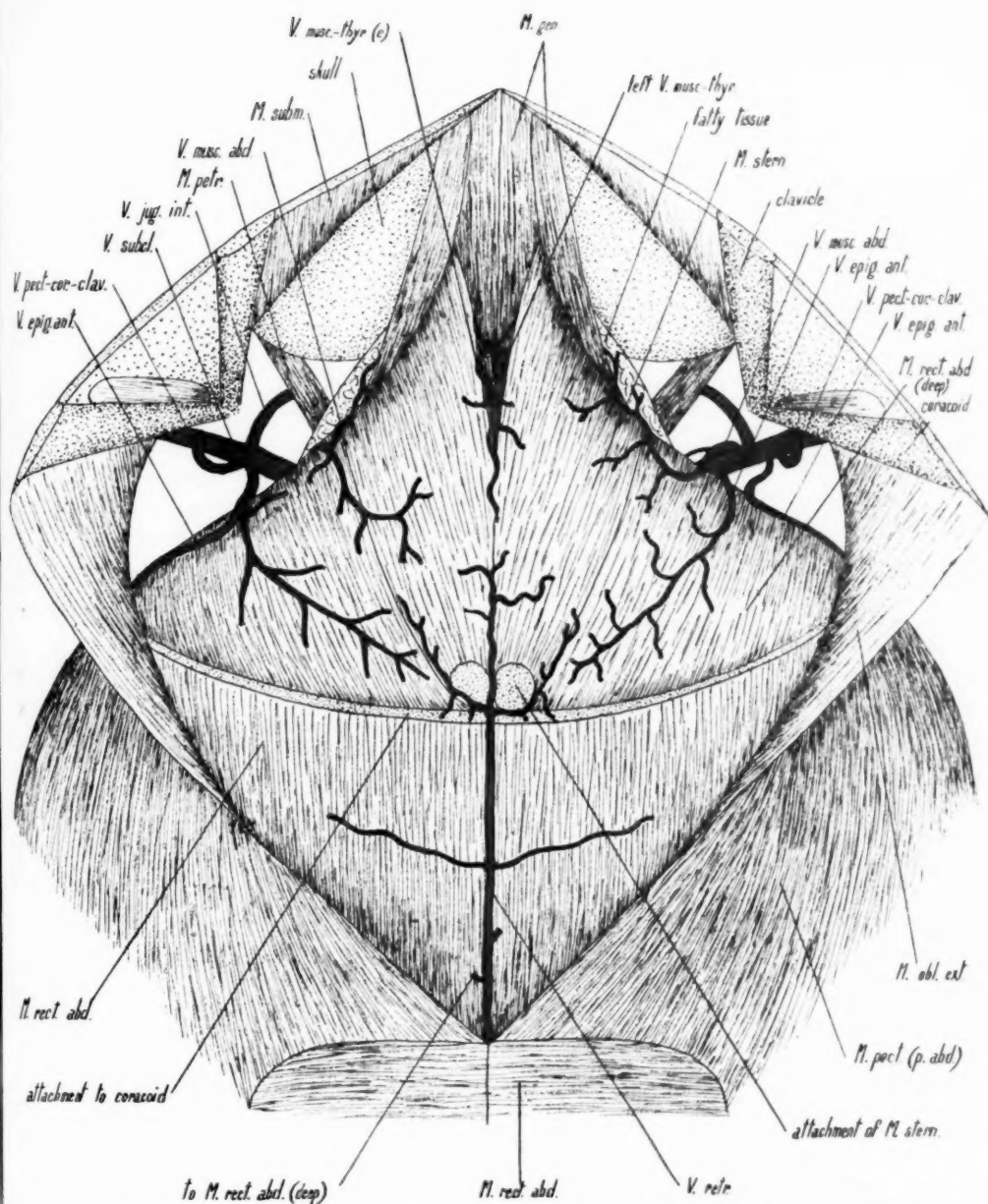


FIG. 13.—A diagram illustrating the venous supply of the ventral musculature. The breast-shoulder apparatus together with *Mm. pectoralis* and *obliquus externus* are folded back on each side. Ventral view. For abbreviations see p. 437.

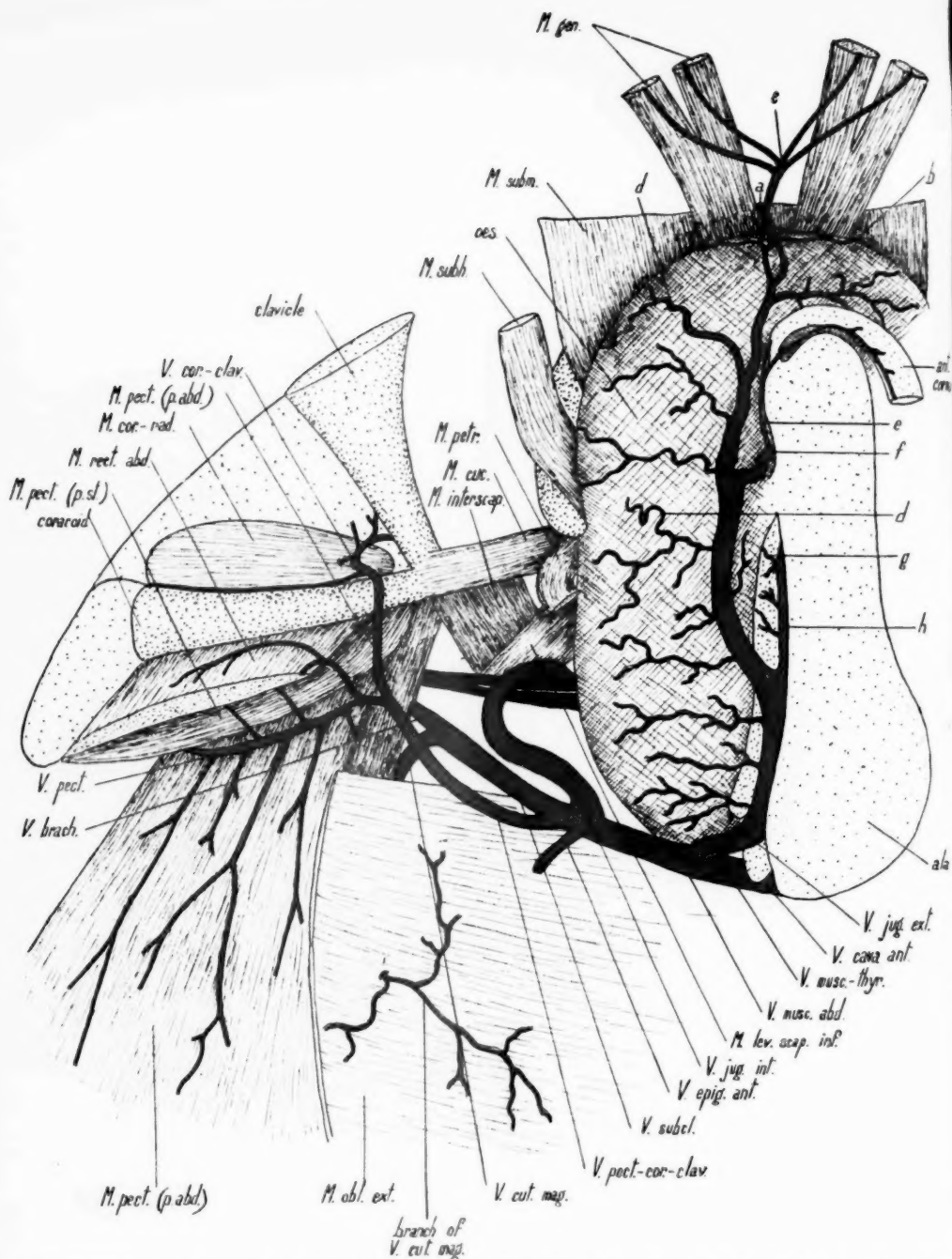


FIG. 14.—A dissection showing the course of the V. cava anterior in the trunk, particularly the branches V. pectoralis-coraco-clavicularis and V. jugularis externa. Ventral view. The heart is removed, the ventral musculature and breast-shoulder apparatus folded to the right, and the hyoid cartilages folded to the left. For branches of V. jugularis externa (a-h) see p. 414, and for other abbreviations p. 438.

V. jugularis interna, passing between M. levator scapulae inferior and M. levator scapulae superior and emerging inside the body-cavity just anterior to the brachial plexus. It then passes backwards as a stout vessel to join the V. subclavia.

(a) *V. orbito-nasalis*. Commences in the anterior region of the head where factors from the nasal capsule, the skin of the olfactory region, and the muscles of the anterior part of the orbit join to form a sinus in front of the orbit. From this the vein passes backwards and ventrally on to the mucous membrane of the roof of the mouth, receiving as it goes smaller branches from the mucous membrane and one from the nasal capsule. It continues backwards below the orbit and optic nerve until it joins the V. ophthalmica in the region of the foramen prooticum.

(b) *V. ophthalmica*. Collects blood from the sclera of the eye, and in addition receives many small branches from the muscles of the orbit and one from the outer surface of the premaxilla. It passes posteriorly and medially to join the V. orbito-nasalis in the region of the foramen prooticum.

The common vein thus formed receives a branch from the ventral part of the eustachian tube and from the mucous membrane of the mouth, and passes inwards through the foramen prooticum together with the N. palatinus. Inside the cranium it lies outside the ganglion prooticum and receives *V. cranialis occipitalis*, *V. cranialis obliqua*, and *V. prosencephali lateralis*, which pass dorsally over the ganglion prooticum to join it.

(c) *V. vertebralis interna dorsalis*. This is a longitudinal vessel situated on the roof of the neural canal, which collects blood from the spinal cord and its cavity. It runs forwards until just behind the skull, where it divides to form the *Vv. craniales occipitales*. These run forward along the side edges of the choroid plexus, receiving several branches from it until each turns outwards to join the V. capitis lateralis in the region of the foramen prooticum. Its branches are as follows:—

- i. *Vv. chorioideae posteriores*. Several branches from the choroid plexus.
- ii. Branches from the interior of the cranium.
- iii. *V. postoccipitalis*. Passes through a foramen on the dorsal surface behind the utriculus and anastomoses with the V. occipitalis.
- iv. A branch passing through a foramen in the roof of the skull from the dorsal musculature of the head.

(d) *V. cranialis obliqua*. From above the cerebral hemispheres, where it anastomoses with its fellow from the opposite side.

(e) *V. prosencephali lateralis*. From the lateral walls of the anterior region of the cranium.

(f). Several branches from the ramifications of the auditory capsule.

(g) *Vv. musculares* from M. temporalis, M. rhomboideus anterior, M. levator scapulae superior, M. cucullaris, M. interscapularis, M. levator scapulae inferior. These are all small veins and show much variation in their arrangement.

(h) *V. facialis*. Collects blood chiefly from the skin of the head and breast, and passes backwards along the side of the head and inwards with the A. cutanea magna to join the V. capitis lateralis soon after it has left the skull. The branches are:

- i. *V. nasalis externa* from the skin of the ventral surface of the tip of the snout, the side of the head, and the region of the external nasal aperture. Also branches from the teeth.
- ii. *V. orbitalis anterior*. A small branch from the anterior-ventral region of the orbit. It drains the Harderian gland and anastomoses with the V. orbito-nasalis.

- iii. *V. cutaneae maxillares*. A number of small branches from the skin of the upper jaw.
 - iv. *V. membranae nictitantis*.
 - v. *V. mandibularis externa* from *M. submaxillaris* with the *A. mandibularis externa* over the outer surface of the lower jaw. It also receives small branches from *M. subhyoideus* and the mucous membrane of the floor of the mouth.
 - vi. *V. infratympanica*. Runs forwards above the lower jaw and below the annulus tympanicus and round the front edge of the *M. depressor mandibulae* to join *V. facialis*. It drains *M. depressor mandibulae*, *M. masseter major*, *M. temporalis*, the lower jaw and the quadrate.
 - vii. *V. cutaneae dorsi* from the skin of the back.
 - viii. *V. cutaneae pectoris* from the skin of the breast.
 - ix. *V. thymica* from the thymus gland and the fatty tissue surrounding it. Also a branch from *M. depressor mandibulae*.
 - x. *V. muscularis* from *M. cucullaris*.
- (i) *V. occipitalis*. Runs backwards over the surface of *M. longissimus dorsi* draining several of the muscles immediately behind the skull. The position where it joins the *V. capitis lateralis* varies from opposite *V. facialis* to opposite *V. vertebralis* (j). It may also join *V. capitis lateralis* in two separate halves.
- i. *V. musculares* from *M. rhomboideus anterior*, *M. longissimus dorsi*, *M. temporalis*, *M. serratus medius*, *Mm. intercostales*.
 - ii. A small branch passing through a foramen on the dorsal surface of the skull and anastomosing with *V. cranialis occipitalis* inside the cranium.
 - iii. A small branch which passes into the marrow-cavities in the base of the skull. From the latter small veins lead into the interior of the cranium and appear to anastomose with *V. cranialis occipitalis*.
 - iv. Made up of small branches coming out of the neural canal with spinal nerves I and II. Runs outwards ventral to the ribs and *M. longissimus dorsi* to join *V. occipitalis*.
- (j) *V. vertebralis*. Collects blood from the muscles of the back and shoulder, from the scapula itself and from the ribs, and runs forward below *M. serratus medius* and *M. serratus superior* to join the *V. capitis lateralis* just before it dives into the interior of the body-cavity as the *V. jugularis interna*.
- i. *V. musculares* from *M. longissimus dorsi* as far as the region of the 8th vertebra. From *M. serratus medius* and *M. serratus superior*.
 - ii. From the scapula.
 - iii. From ribs 3 and 4.

Vena subclavia (text-figs. 4 and 14).

The *V. subclavia* is made up by the junction of the *V. cutanea magna* and the *V. brachialis* just posterior to the point where the brachial plexus passes through to the arm. It passes inwards and slightly backwards to join the *V. cava anterior*. It receives also two smaller veins—*V. pectoralis-coraco-clavicularis* and *V. epigastrica anterior*—just before it joins the *V. cava anterior*.

Vena epigastrica anterior (text-figs. 13 and 14).

Collects blood from *M. rectus abdominis* (deep portion) and *M. transversus* and runs forward to join the *V. subclavia* almost opposite the *V. jugularis interna*. It may anastomose (i) with *V. muscularis abdominis* on the outer surface of *M. rectus abdominis* or (ii) with a muscular branch of the *V. abdominalis* on the inner surface of *M. rectus abdominis*.

Vena pectoralis-coraco-clavicularis (text-fig. 14).

This vein is made up by the junction of the *V. coraco-clavicularis* and *V. pectoralis* and enters the *V. subclavia* just before the *V. jugularis interna*. In rare cases the two branches open separately into the *V. subclavia*. In *Rana* the two are completely separate, the *V. coraco-clavicularis* entering the *V. subclavia* and the *Vv. pectorales* entering the *V. cutanea magna*.

V. coraco-clavicularis receives branches from *M. deltoideus*, *M. mylopectori-humeralis*, *M. scapulo-humeralis profundus anterior*, *M. scapulo-humeralis profundus posterior*, *M. coraco-radialis*, *M. supracoracoideus medius*, *M. supracoracoideus posticus*, *M. coraco-brachialis longus*, *M. pectoralis* (portio sterno-coracoidea), the coracoid, clavicle and glenoid cavity. The vein passes inwards through the fenestra between the procoracoid and the coracoid and backwards to join the *V. pectoralis*.

V. pectoralis receives branches from the skin, *M. pectoralis* (portio abdominalis), *M. obliquus externus*, *M. supracoracoideus posticus*, *M. pectoralis* (portio sterno-coracoidea), *M. rectus abdominis* (superficial portion).

Vena cutanea magna (text-figs. 4 and 14).

This vein collects blood from the skin of the back and belly, runs forwards and dives into the side of the body between *M. latissimus dorsi* and *M. pectoralis* (portio abdominalis). Inside the body-cavity it receives the *V. dorsalis scapulae posterior* and joins the *V. brachialis* to form the *V. subclavia*.

It differs from the corresponding vein in *Rana* in that (a) it does not include the *V. facialis* (see *V. jugularis interna*), (b) the main flow of blood in the surface of the skin is cranialwards and not caudalwards, and (c) it receives the *V. dorsalis scapulae posterior*, which in *Rana* joins the *V. subscapularis*.

The branches are:

- (a) *Vv. cutaneae dorsi* from the skin of the back.
- (b) *Vv. cutaneae abdominis* from the skin of the ventral surface.
- (c) *Vv. musculares* from *M. obliquus externus* and *M. transversus*.
- (d) *V. dorsalis scapulae posterior* from *M. latissimus dorsi*, *M. dorsalis scapulae*, and *M. obliquus externus*.

Vena brachialis (text-fig. 15).

The veins of the arm in *Xenopus* are very different from those in *Rana*. In the first place, the *V. subscapularis* is entirely absent; and secondly, the course of the *V. brachialis* itself is quite different.

The blood from the digits, wrist, and forearm is collected by the *V. interossea*, which lies on the ventral surface of the forearm below *M. flexor carpi ulnaris* and *M. flexor carpi radialis*, and in close proximity to the *A. interossea* and *N. brachialis longus inferior*. At the wrist the *V. interossea* communicates with the *arcus venosus dorsi manus* and with *V. cutanea antibrachii medialis superior*. Along its course it receives branches from *M. palmaris longus*, *M. epitrochleo-cubitalis*, the radius and ulna, *M. flexor carpi radialis*, *M. flexor carpi ulnaris*, *M. flexor antibrachii lateralis superficialis*, *M. extensor carpi ulnaris*, *M. epicondylo-cubitalis*, *M. anconaeus* (*caput mediale*).

At the elbow the *V. interossea* emerges from beneath *M. flexor carpi radialis* on the inner surface of the arm as the *V. brachialis*. At this point it is joined by the *V. cutanea antibrachii medialis superior*. It runs forwards over *M. deltoideus* to the anterior surface of the arm where it is joined by the *V. superficialis antibrachii*. It then passes round the anterior surface of *M. deltoideus* and runs proximally along the outer surface of the upper arm, in this part of its course lying close to *A. profunda brachii* and *N. radialis*. Just next to the attachment of *M. latissimus dorsi* and *M. dorsalis scapulae* it turns backwards and crosses *M. anconaeus* (*caput laterale* and *caput scapulare*) to join the *V. cutanea magna* just behind the arm.

Branches of V. brachialis.

- (a) *V. cutanea antibrachii medialis superior* from the skin of the ventral forearm. Anastomoses with *V. interossea* at the wrist. Receives small branches also from *M. flexor antibrachii lateralis superficialis*.
- (b) *V. superficialis antibrachii*. Carries blood from the *arcus venosus dorsi manus*, which circles the wrist below the superficial muscles and collects blood from the digits, and joins the *V. brachialis* on the anterior surface of the upper arm. Also receives several cutaneous branches from the skin of the anterior-dorsal forearm.
- (c) *Vv. musculares* from *M. deltoideus*, *M. extensor carpi radialis*, *M. dorsalis scapulae*, *M. anconaeus* (*caput profundum*, *caput laterale*, and *caput scapulare*).
- (d) A cutaneous branch from the skin of the dorsal fore and upper arm, joining *V. brachialis* just anterior to *V. superficialis antibrachii*.
- (e) One or two branches from the skin of the dorsal upper arm (small) joining *V. brachialis* just above *M. anconaeus* (*caput laterale*).

Vena cava posterior (text-figs. 16 and 17).

In the posterior part of its course the *V. cava posterior* lies between the kidneys on the ventral surface of the aorta abdominalis. Here it

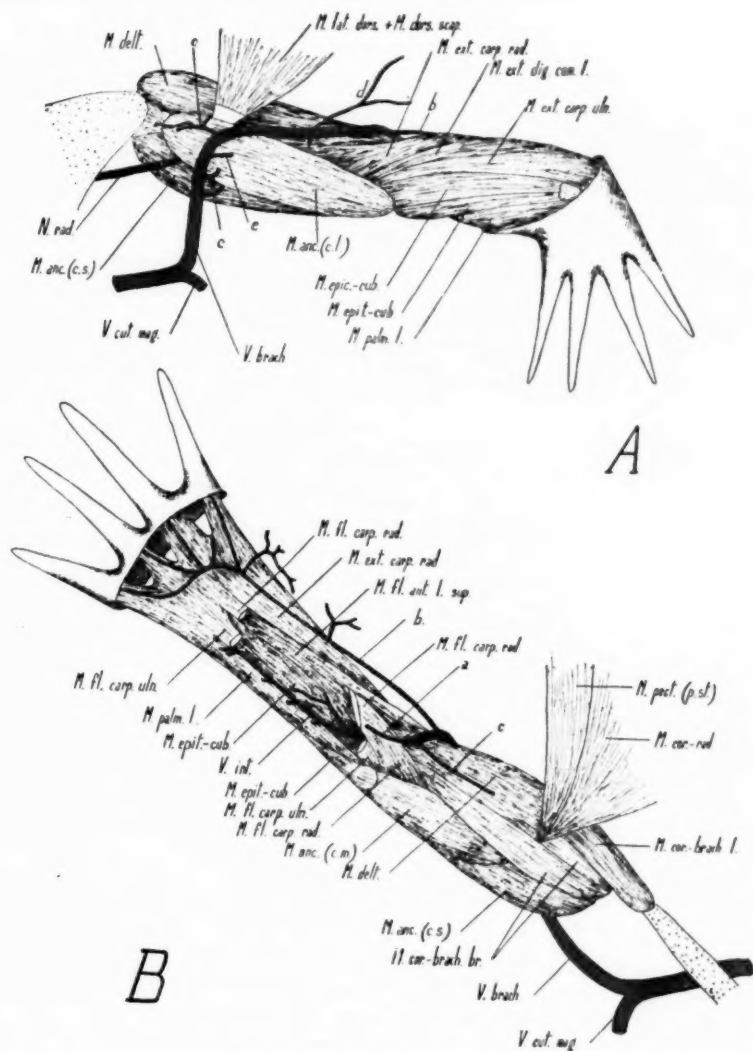


FIG. 15.—The course of the V. brachialis in the fore-limb; A, an outer view, and B, an inner view. For branches of V. brachialis see p. 420, and for other abbreviations p. 438.

receives the blood from the kidneys through a number of Vv. renales revchentes on each side and from the ovary or testis through the

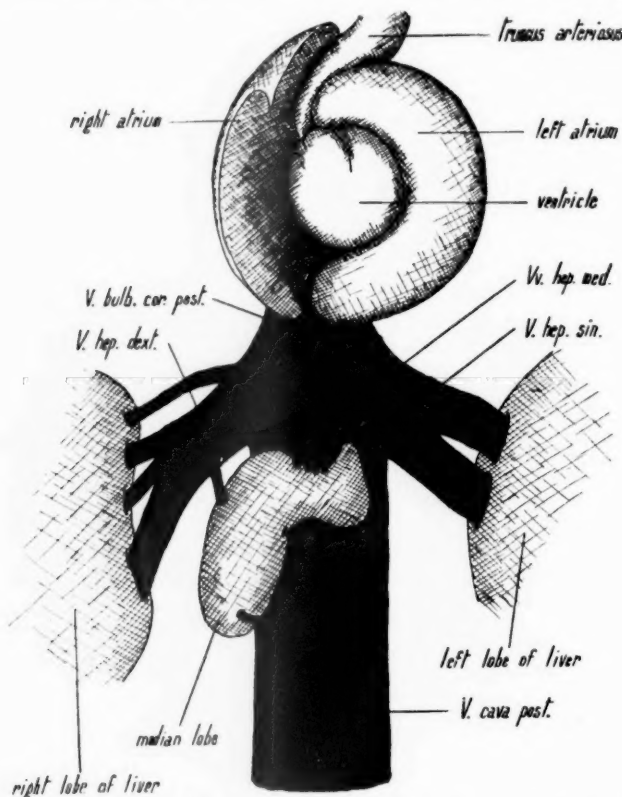


FIG. 16.—A diagram showing the entrance of the V. cava posterior and Vv. hepaticae into the heart. Ventral view. The heart is tilted forwards to show the course of the V. bulbi cordis posterior. For abbreviations see p. 437.

Vv. genitales. It runs forwards over the dorsal surface of the liver and receives the stout Vv. hepaticae just before it empties itself into the sinus venosus. Into the sinus venosus itself opens the small V. bulbi cordis posterior from the bulbus cordis.

Vena bulbi cordis posterior (text-fig. 16).

Leaves the bulbus cordis and runs along the dorsal surface of the ventricle between the two auricles, to enter the sinus venosus in the mid-

ventral line. In *Rana* the V. bulbi cordis posterior joins the V. abdominalis, a condition which will be discussed later (see p. 435).

Venae hepaticae (text-fig. 16).

The Vv. hepaticae consist of two large trunks carrying blood from the right and left lobes of the liver and several smaller veins from the median lobe. The V. hepatica sinistra and the V. hepatica dextra from the left and right lobes respectively are both formed by the confluence of two or three large veins out of the substance of the liver. There are usually approximately four Vv. hepaticae mediae passing from the median lobe into the V. cava posterior, but these vary considerably both in number and position. There may be branches opening into the V. hepatica sinistra or the V. hepatica dextra.

Venae renales revehentes (text-fig. 17).

From the substance of each kidney into the V. cava posterior pass a number of Vv. renales revehentes. The number varies from 5 to 8 in the female and from 6 to 10 in the male. The hindermost one is usually the stoutest.

Venae genitales (text-fig. 17).

These consist in the female of from 4 to 5 Vv. ovaricae leading from the ovary on each side into the V. cava posterior. In the male there are from 3 to 5 Vv. spermaticae from the testis opening into the V. cava posterior or the Vv. renales revehentes. In both sexes the foremost V. genitalis usually anastomoses with the V. corporis adiposi.

Vena corporis adiposi (text-fig. 17).

From each fatty body come one or two Vv. corpora adiposa to open into the V. cava posterior direct or into one of the Vv. renales revehentes.

HEPATIC PORTAL SYSTEM.

A. *Vena abdominalis* (text-fig. 18).

The V. abdominalis commences in the region of the cloaca, where it is made up by the junction of the right and left Vv. abdominales posteriores. The latter form anastomoses with the Vv. ischiadicae. The V. abdominalis passes forwards along the ventral surface of the pelvic cavity until, dorsal to the epipubic cartilage, it receives the Vv. abdominales anteriores. These branches anastomose with the right and left Vv. femorales and correspond to the Rami abdominales or pelvic veins of *Rana*. The V. abdominalis then continues forwards along the linea alba on the dorsal surface of M. rectus abdominis, receiving a series of paired branches from the latter. In the region of the 4th inscriptio tendinea (reckoning

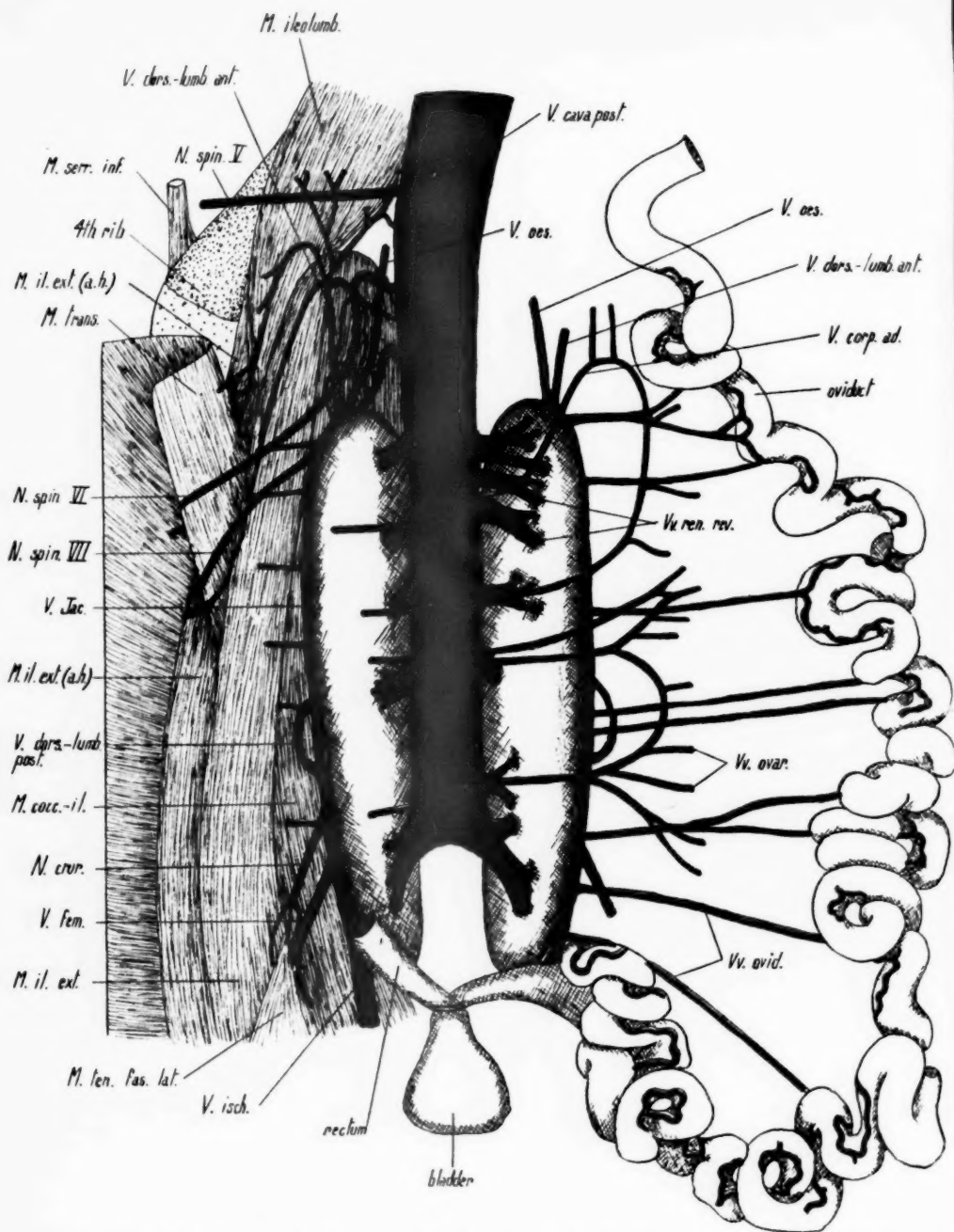


FIG. 17.—A dissection showing the course of the V. cava posterior, the Vv. genitales on the right, and the Vv. renales adhehentes secundariae on the left. Ventral view. For abbreviations see p. 437.

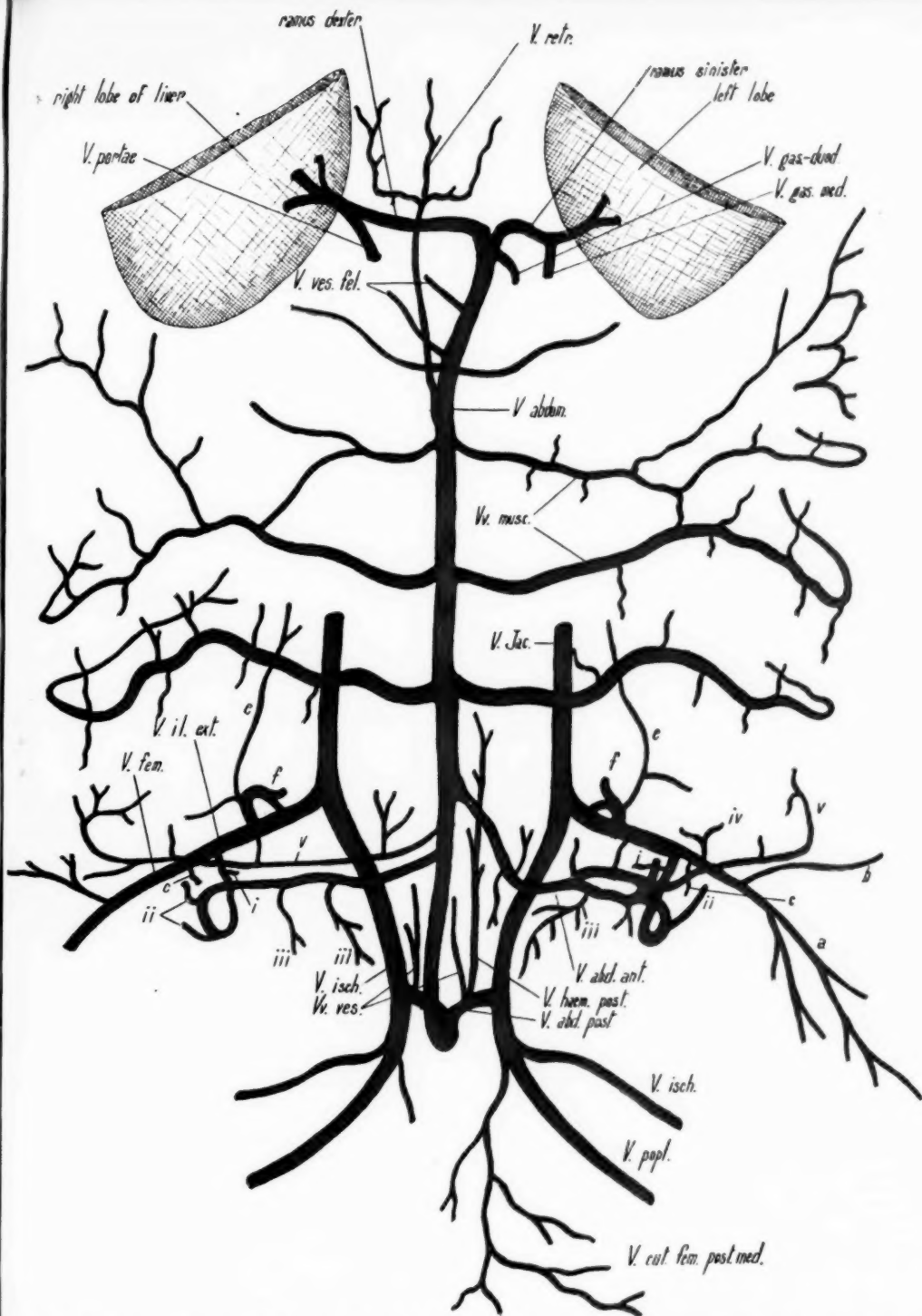


FIG. 18.—A diagram showing the branches of the V. abdominalis and its communications with the hind-limb veins. Ventral view. For branches of V. abdominalis anterior (i-v) see p. 426, branches of V. iliaca externa (a-f) p. 428, and other abbreviations p. 438.

from behind) it receives the V. retrosternalis and leaves the ventral body-wall to run dorsally towards the liver. It receives one or more branches from the gall-bladder and divides into a ramus dexter and a ramus sinister, which anastomose with branches of the V. portae hepatis and enter the right and left lobes of the liver respectively.

The branches are as follows:—

- (a) *Vv. abdominales posteriores*. These are two short thick branches which leave the Vv. ischiadicae in the region of the cloaca and join to form the V. abdominalis on the ventral surface of the cloaca dorsal to the pubic symphysis. They are not present in *Rana*, but have already been described for *Xenopus*, as "pelvic veins" by Dreyer and Gilchrist and von Bonde, and "Vv. vesicales" by Grobbelaar. They receive several small branches.
 - i. *Vv. vesicales* from the bladder. One to three branches.
 - ii. *V. haemorrhoidalis posterior*. From the rectum and cloaca. Enters the right or left V. abdominalis posterior. In *Rana* this vein enters the V. ischiadica, and has connections with the hepatic portal system.
- (b) *Vv. abdominales anteriores*. These branches leave the Vv. femorales on the ventral surface of the M. iliacus internus and run ventrally and then medially to join the V. abdominalis in the region of the epipubic cartilage. They correspond to the rami abdominales of *Rana* (pubic veins of Dreyer, pelvises of Grobbelaar). They receive the following branches:—
 - i. *V. muscularis* from M. pectineus and M. iliacus internus.
 - ii. *V. cutanea abdominis* from the skin of the ventral body-wall and ventral upper thigh. Anastomose with V. cutanea magna.
 - iii. *Vv. musculares*. 2 or 3 muscular branches together draining M. pectineus, M. obturator externus, M. sartorio-semi-tendinosus, M. adductor magnus (caput dorsale and ventrale), M. quadratus femoris, M. semimembranosus.
 - iv. *Vv. musculares* from M. rectus abdominis (small).
 - v. *V. cutanea femoris anterior medialis*. This vein runs medially along the first inscriptio tendinea (reckoning from behind) to join either the V. abdominalis anterior or the V. abdominalis itself. It varies somewhat in its course and may form a plexus with the V. abdominalis anterior. It drains the skin of the ventral upper thigh and ventral body wall and the muscles of the ventral body wall, including M. transversus and M. rectus abdominis.
- (c) *Vv. musculares* from M. rectus abdominis. These consist of three pairs of veins running medially along the inscriptiones tendineae (nos. 2-4 reckoning from behind) to join the V. abdominalis in the mid-ventral line. They drain the lateral and ventral body-wall, including M. rectus abdominis (deep and superficial), M. transversus, M. pectoralis (portio abdominalis), M. obturator externus.
- (d) *V. retrosternalis* from the dorsal surface of the sternum and the muscles in that region, joining V. abdominalis in the region of the 4th inscriptio tendinea (reckoning from behind). It collects blood from M. sternohyoideus and M. rectus abdominis (deep and superficial). It may anastomose with branches of the V. cava anterior, either with V. muscularis-thyroidea in the mid-line, with V. muscularis abdominis along the outer edge of M. sternohyoideus, or with V. pectoralis.
- (e) *Vv. vesicae felleae*. 1-3 branches from the gall-bladder, joining V. abdominalis as it passes ventrally to the liver.

B. *Vena portae hepatis* (text-fig. 6).

The description given here is for the normal condition, but it must be borne in mind that the portal veins in *Xenopus* are subject to a considerable amount of variation.

The three main portal veins do not join to form a single system as in *Rana* but enter the liver independently. The main V. portae itself collects blood from the posterior part of the intestine, receives the V. gastrica anterior, and anastomoses with the ramus dexter of the V. abdominalis to enter the right lobe of the liver. On the way it gives off a few small branches to the median lobe. The V. gastrica media and V. gastrica duodenalis anastomose with the ramus sinister of the V. abdominalis and empty themselves into the left lobe of the liver. The branches are as follows:—

- (a) *V. portae* (main stem). Receives the following branches:—
 - i. *Vv. intestinales* from the posterior half of the intestine. These anastomose with one another on the surface of the gut.
 - ii. *Vv. haemorrhoidales anteriores* from the anterior portion of the rectum.
 - iii. *Vv. lienales*. 1–4 short branches from the spleen.
 - iv. *V. gastrica anterior*. A large branch from the dorsal anterior region of the stomach and pancreas, entering the V. portae at the point where it passes the pancreas.
- (b) *V. gastro-duodenalis*. A large branch from the posterior end of the stomach, from the pancreas and from the duodenum. It enters the ramus sinister of the V. abdominalis. It consists of:
 - i. *V. gastrica posterior* from the pylorus and the posterior dorsal region of the stomach.
 - ii. *V. duodenalis anterior* from the duodenum anastomosing with the Vv. intestinales.
 - iii. *Vv. pancreaticae* from the pancreas.
- (c) *V. gastrica media*. A well-developed vein from the pancreas and the ventral medial region of the stomach. It enters the ramus sinister of the V. abdominalis.

RENAL PORTAL SYSTEM (text-figs. 17–19).

The renal portal system is made up chiefly by the veins from the leg. The V. ischiadica and V. iliaca externa open into the V. Jacobsonii, a stout vein which runs along the dorsal outer edge of the kidney and lies lateral and dorsal to the ureter. (N.B.—There is no V. iliaca communis in *Xenopus*.) Into the lateral edge of the V. Jacobsonii open the Vv. renales advehentes secundariae, which consist of V. dorso-lumbalis anterior, V. dorso-lumbalis posterior, Vv. oviducuales (in the female), and the V. oesophagea. From the medial edge of the V. Jacobsonii are given off the Vv. renales advehentes. These branch and break up into capillaries in the kidneys. The Vv. renales advehentes secundariae are as follows:—

- (a) *V. dorso-lumbalis anterior*. This vein is made up of a number of branches in the region of the 5th vertebra. It runs backwards ventral to nerves 5 and 6 to join the *V. Jacobsonii* at the anterior end of the kidney. Sometimes it enters the kidney direct. The branches vary tremendously. They collect blood from the following muscles: *M. transversus*, *M. ileolumbaris*, *M. iliacus externus*, *M. iliacus externus* (accessory head), *M. longissimus dorsi*, *M. coccygeo-iliacus* and *M. obliquus externus*. It also receives blood from the surface of the ileum and the vertebral column. Besides these there is a longitudinal branch lying ventral to the ribs and next to the vertebral column. The latter is almost always present, and receives branches from the neural canal along with spinal nerves 4-7 and sometimes also with 3 and 8 (*V. intervertebralis communis*).
- (b) *V. dorso-lumbalis posterior*. Receives blood chiefly from *M. coccygeo-iliacus* in the region of the sciatic plexus and joins the *V. Jacobsonii* about half-way up its course. It may join one of the *Vv. renales advehentes* instead of the *V. Jacobsonii*. Occasionally it is absent altogether. Also receives branches from the sacral diapophysis, *M. longissimus dorsi*, spinal nerves 7, 8, and 9; and branches leave the neural canal with spinal nerves 8 and 9.
- (c) *V. oesophagea*. From the dorsal surface of the oesophagus and anterior region of the stomach. Joins *V. Jacobsonii* at the anterior end of the kidney next to *V. dorso-lumbalis anterior*. Sometimes absent.
- (d) *Vv. oviducalae* (in female only). From 7 to 10 long thin veins from the oviduct.

Vena femoralis and Vena iliaca externa (text-fig. 18).

The *V. femoralis* is the main vein of the leg in *Rana*, but in *Xenopus* it is very much reduced and only drains the skin and a few muscles of the upper thigh. This is taken to be a primitive condition. It is also probable, as mentioned by Grobbelaar, that the femoral vein has only secondarily become the important blood-vessel that it is in *Rana*. The vein collects blood from *M. cruralis* and runs forwards between *M. tensor fasciae latae* and *M. cruralis*. It receives the *V. abdominalis anterior* at the point where *M. iliacus internus* and *M. cruralis* adjoin, and continues as the *V. iliaca externa*. The latter runs medially and anteriorly to join the *V. ischiadica* at the posterior end of the kidney. The branches are:

- (a) *V. muscularis* from *M. cruralis*.
- (b) *V. cutanea femoris lateralis*. From the skin of the anterior-dorsal thigh, with *A. cutanea femoris lateralis*, but passing under *M. tensor fasciae latae* to join *V. femoralis*. Also from *M. tensor fasciae latae*, *M. pectoralis* (portio abdominalis), and *M. transversus*.
- (c) *V. muscularis* from *M. iliacus internus*.
- (d) *V. abdominalis anterior*. See *V. abdominalis*.
- (e) *V. muscularis* from *M. iliacus externus* and *M. tensor fasciae latae*. Joins *V. iliaca externa*.
- (f) A deep vein from *M. iliacus externus*, *M. iliacus externus* (accessory head), *M. iliacus internus*, and the ileum.

Vena ischiadica (text-fig. 19).

The V. ischiadica itself is a comparatively short vein and very similar to that of *Rana*. It collects blood from the muscles of the thigh and in its course lies ventral to A. ischiadica and N. ischiadicus. In the proximal region of the thigh it receives the strong V. poplitea from the lower leg, turns forwards, and dives into the pelvic cavity just behind the tendon of the M. gluteus magnus. It then continues forwards until it joins the V. Jacobsonii at the posterior end of the kidney.

V. poplitea. The main vein of the lower leg begins in the foot as the V. dorsalis pedis, which collects blood from the foot and digits and passes forwards over the dorsal surface of the foot. At the ankle it receives more branches from the muscles and skin of the leg. Then just as in *Rana* it passes under the caput peroneale of the M. tibialis anticus longus and M. peroneus into the calf to form the V. peronea, which passes forwards under M. plantaris longus close to the A. peronea anterior superior. Near the knee it receives the V. circumflexa genu lateralis inferior and becomes the V. poplitea. This vein, after receiving several more branches from the muscles and skin of the calf, passes into the thigh ventral to the tendons of M. plantaris longus and M. semimembranosus in close proximity to A. poplitea. In the thigh it does not join the V. femoralis as in *Rana*, but continues its course between M. ileo-fibularis and M. semimembranosus close to A. ischiadica along the distal half of the thigh. After this it becomes more superficial, lying between M. semimembranosus and M. gluteus magnus, until in the proximal end of the thigh it empties itself into the V. ischiadica.

Branches of V. dorsalis pedis (in ankle region only).

- (a) *V. cutanea dorsi pedis lateralis*. From skin of dorsal foot. Joins V. dorsalis pedis at proximal end of foot.
- (b) *V. cutanea cruris anterior inferior* (in Gaupp a branch of V. intermalleolaris anterior). From skin of anterior-dorsal calf. Joins V. dorsalis pedis opposite (a) and between the two heads of M. tibialis anticus longus.
- (c) *V. cutanea cruris lateralis inferior*. From skin of posterior-dorsal calf, with small branches from M. peroneus, the muscles of the foot, M. tibialis anticus longus, and the ankle joint. Passes in between M. peroneus and M. tibialis anticus longus to join V. dorsalis pedis. (In *Rana* it passes between M. peroneus and M. plantaris longus.)
- (d) *V. muscularis* from M. tibialis anticus longus (both heads).
- (e) *V. malleolaris medialis*. Receives branches from the skin of the ventral calf, the ankle joint, foot muscles, M. plantaris longus, M. extensor cruris brevis, M. tibialis anticus brevis, M. tibialis anticus longus. Emerges from beneath M. extensor cruris brevis and M. tibialis anticus brevis to join V. dorsalis pedis at the distal end of the calf.

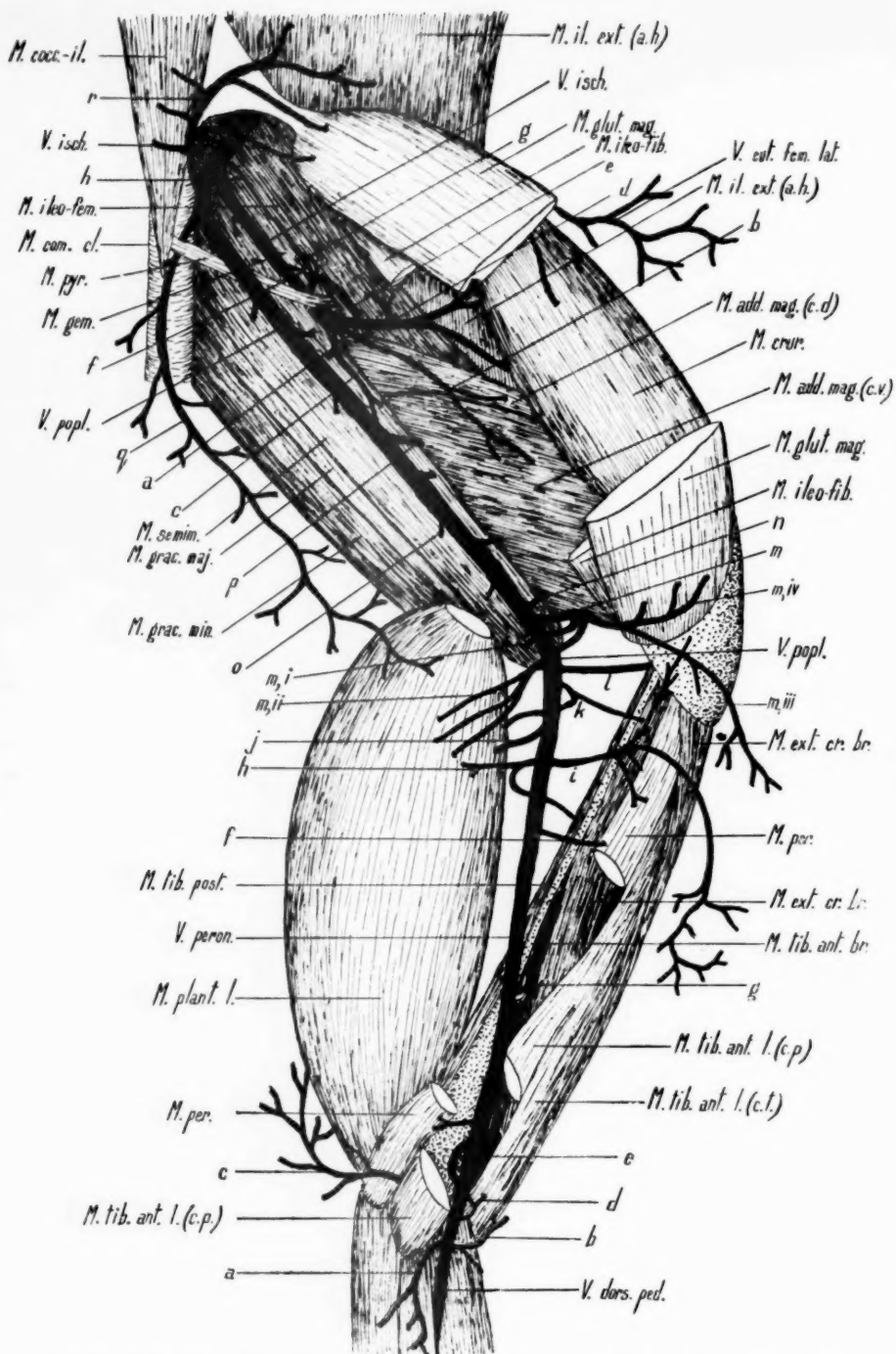


FIG. 19.—A dissection of the veins of the hind-limb viewed from the dorsal surface. For branches of *V. poplitea* and *V. ischiadica* see pp. 431–432, and for other abbreviations p. 438.

Branches of V. peronea.

- (f) *Vv. musculares* from M. peroneus.
- (g) *V. muscularis* from M. extensor cruris brevis, M. tibialis anticus brevis, and M. tibialis posticus.

Branches of V. poplitea.

- (h) *V. suralis muscularis* from M. plantaris longus and M. tibialis posticus. Joins V. poplitea in the proximal end of the calf.
- (i) *V. circumflexa genu lateralis inferior.* From the knee-joint, M. peroneus, M. extensor cruris brevis, M. tibialis anticus longus, and sometimes from the skin of the anterior-dorsal calf (*V. cutanea cruris anterior superior*). It joins V. poplitea in the proximal region of the calf, opposite (h).
- (j) *V. tibialis posterior.* Close to corresponding artery. From the medial surface of M. plantaris longus. Joins V. poplitea just anterior to (h) and (i).
- (k) *Vv. musculares* from M. plantaris longus and M. extensor cruris brevis.
- (l) *V. circumflexa genu medialis inferior.* With artery of same name. From the skin of the ventral calf (*V. cutanea genu medialis inferior*) and posterior ventral thigh. From the ventral knee-joint, M. extensor cruris brevis, M. plantaris longus, and attachments of M. sartorio-semitendinosus, M. gracilis major, M. gracilis minor, M. cruralis, M. semimembranosus. Joins V. poplitea below the tendon of M. plantaris longus.
- (m) *V. circumflexa genu lateralis superior.* Runs with A. suralis communis to join V. poplitea at the distal end of the thigh. Consists of several branches:—
 - i. *V. cutanea cruris posterior.* From the skin of the posterior-dorsal calf, with artery of same name.
 - ii. *V. muscularis* from M. plantaris longus.
 - iii. *V. cutanea genu et cruris lateralis superior.* From skin of dorsal knee and anterior-dorsal calf. With artery of same name.
 - iv. From skin of anterior-dorsal thigh and from M. gluteus magnus.
- (n) *V. circumflexa genu medialis superior.* With artery of same name. From skin of ventral thigh (*V. cutanea genu medialis superior*—not always present), M. adductor magnus (caput ventrale and caput dorsale), M. sartorio-semitendinosus, the femur, M. semimembranosus, the knee-joint, M. cruralis. Joins V. poplitea just anterior to (m).
- (o) *Vv. musculares* from M. semimembranosus.
- (p) *Vv. musculares* from M. gluteus magnus, and M. ileo-fibularis.
- (q) *V. cutanea femoris posterior medialis.* (A branch of V. ischiadica in *Rana*.) From the skin of the posterior thigh, with small branches from the skin of the cloaca. Runs under M. pyriformis to join V. poplitea in the proximal region of the thigh.
- (r) *V. iliaca transversa.* Joins the V. poplitea opposite (q). It is not connected to the V. femoralis as in *Rana*. It receives the following branches:—
 - i. *Vv. musculares* from M. latissimus dorsi, M. obliquus externus, M. iliacus externus (accessory head), M. gluteus magnus, M. coccygeo-iliacus.
 - ii. *Vv. coccygeae superficiales* from the skin of the back above the os coccygis and the proximal dorsal thigh. Anastomose with V. cutanea magna.
 - iii. *Vv. cordis lymphatici posteriores* from the posterior lymph hearts.

Branches of V. ischiadica.

- (a) *V. profunda femoris posterior*. A deep vein in the middle region of the thigh. Emerges between *M. adductor magnus* (caput dorsale) and *M. semimembranosus*. From *M. semimembranosus*, *M. gracilis major*, *M. gracilis minor*, *M. sartorio-semitendinosus*. May be double.
- (b) *V. muscularis* from *M. adductor magnus* (caput dorsale and caput ventrale).
- (c) *V. muscularis* from *M. semimembranosus*.
- (d) *V. muscularis* from *M. gluteus magnus*, *M. cruralis*, *M. ileo-femoralis*, *M. ileo-fibularis*, *M. adductor magnus* (caput dorsale), *M. iliacus externus* (accessory head), *M. iliacus internus* (at attachment to femur).
- (e) *V. circumflexa femoris medialis secunda*. A deep vein lying below *M. adductor magnus* (caput dorsale). From *M. adductor magnus* (caput dorsale and caput ventrale), *M. ileo-femoralis*, and the surface of the femur.
- (f) *V. circumflexa femoris medialis prima*. Emerges from between *M. gemellus* and *M. quadratus femoris* to join *V. ischiadica* just opposite (e). From *M. obturator externus*, *M. quadratus femoris*, *M. gemellus*, *M. adductor magnus* (caput dorsale), *M. obturator internus*, the acetabulum and femur.
- (g) *V. muscularis*. Emerges from between *M. gemellus* and *M. ileo-femoralis* to join *V. ischiadica* opposite (e) and (f). From *M. gemellus*, *M. ileo-femoralis*, and *M. iliacus externus* (accessory head).
- (h) *V. muscularis* from *M. gemellus*, *M. quadratus femoris*, and *M. ileo-femoralis*. Joins *V. ischiadica* just before its junction with *V. poplitea*.

DISCUSSION.

When comparing the anatomy of *Xenopus* with that of one of the terrestrial Anura, as, for instance, *Rana*, it is found that the main plan of the blood-vessels in the two animals is the same. There are, however, certain characteristics that defy comparison and are difficult to account for. In these cases similarities can often be found not among the advanced land Amphibia but among the Urodeles; and such features immediately assume significance when we consider the position of the Aglossa among the Amphibia. Particularly interesting from this point of view is the venous system.

In the veins of the hind-limb of *Xenopus* the main blood-stream from the lower leg flows into the post-axial vein or *V. ischiadica*, and not into the *V. femoralis* as in *Rana*. The latter vein is much reduced and conveys blood only from a few muscles and the skin of the upper thigh. Grobbelaar (1924) has already drawn attention to this fact and emphasises that it is a primitive condition and that "the femoral vein in *Rana* has only secondarily become the important blood-vessel which it is."

If we consider next the conditions in *Salamandra* (Francis, 1934) we find that here also the main blood-stream from the leg flows directly into the post-axial vein or *V. ischiadica*, and that this vein represents the continuation of the renal portal vein. In *Salamandra* there is no pre-axial vein from the leg, but there is a well-developed pelvic vein on each side

passing from the renal portal vein to the V. abdominalis. It is also connected to the V. ischiadica by the V. iliaca transversa. These pelvic veins apparently represent the posterior ends of the lateral veins of the embryo, which fuse anteriorly to form the V. abdominalis. This point, however, would have to be verified from the embryology. It appears, then, that in higher forms each pelvic vein develops a pre-axial branch from the leg which becomes the V. femoralis, and the connection with the V. abdominalis becomes reduced to a narrow anastomosis.

In *Xenopus* the pre-axial vein is present as the V. femoralis. The post-axial vein has split into two parts: (a) the main vein conveying blood from the lower part of the leg (V. poplitea), and (b) the smaller and much-branched vein collecting blood from the muscles of the thigh. These two veins join at the proximal end of the thigh (see text-fig. 19).

In *Rana* the main vein of the leg is pre-axial. This state of affairs could easily be explained by the assumption that branch (a) of the post-axial vein of *Xenopus* has become disconnected and reconnected with the pre-axial vein or V. femoralis. Branch (b) remains as a comparatively short V. ischiadica collecting blood from the thigh.

It appears, therefore, that the arrangement of the hind-limb veins in *Rana* is secondary, while that in *Xenopus* represents something intermediate between conditions found in the Urodeles and the Phaneroglossa. This is in keeping with the admitted neotenic origin of the Aglossa.

The structure of the abdominal veins in *Salamandra* can also be profitably compared with that in *Xenopus*, for in both types there are two anastomoses between the abdominal veins and the renal portal system (see text-fig. 20). In *Salamandra* the anterior anastomosis is the well-developed pelvic vein. The abdominal vein, however, continues backwards as the narrow V. cloacae medialis, which in the region of the cloaca divides to form the two Vv. pudendae. These anastomose on either side with the Vv. ischiadicae. The anterior anastomosis is obviously homologous with the V. abdominalis anterior of *Xenopus*, and the posterior anastomosis could easily be compared with the V. abdominalis posterior.

Another interesting problem in *Xenopus* is the presence of the two well-developed veins on each side draining the region of the hyoid apparatus and floor of the mouth, namely, the V. jugularis externa and the V. muscularis-thyroidea (text-figs. 12 and 14). Again light can be thrown on the matter by referring to conditions in the Urodeles.

The V. jugularis externa of *Salamandra* develops from the V. jugularis inferior of the embryo and consists of three elements:

- i. *V. facialis communis*, collecting blood from the orbit, the superficial intermandibular region and the thymus.
- ii. *V. lingualis*, collecting blood from the region of the tongue and hyoid

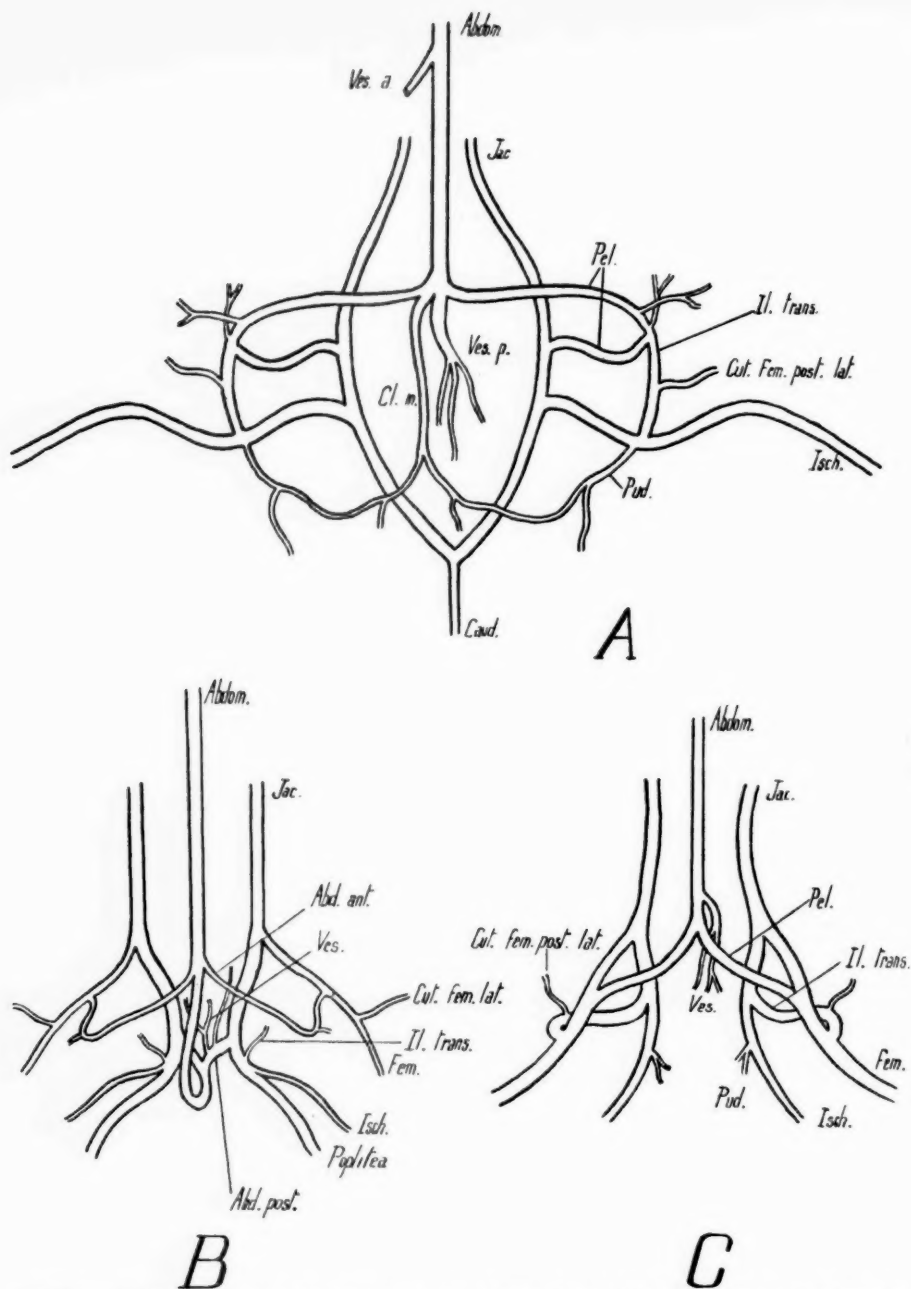


FIG. 20.—A diagram showing the structure of the abdominal and hind-limb veins in A, *Salamandra salamandra* (from Francis), B, *Xenopus laevis*, and C, *Rana esculenta* (from Gaupp). For abbreviations see p. 437.

apparatus, and passing *dorsal* to the hyoid apparatus and the arterial arches to join the V. jugularis externa.

- iii. V. *thyroidea*, collecting blood from the thyroid gland and connective tissue around it, with a branch from the skin, and passing *ventral* to the hyoid apparatus and arterial arches to join the V. lingualis.

Of these the V. *facialis communis* is absent in the Anura. The V. *lingualis* and V. *thyroidea* are homologous with the V. *jugularis externa* and the V. *muscularis-thyroidea* respectively of *Xenopus*, the only difference being that in *Xenopus* the V. *muscularis-thyroidea* passes *dorsal* to the arterial arches instead of *ventral*. In both forms the lingual element is the main one, and runs *dorsal* to the hyoid apparatus. In *Xenopus* the two veins are connected by several anastomoses. In *Rana* the dorsal element has apparently disappeared, while the ventral or thyroid element takes over the main blood-stream from the hyoid apparatus and is known as the V. *jugularis externa*.

It may be pointed out here that these similarities between *Salamandra* and *Xenopus* do not necessarily imply any close affinity of the two groups, but merely tend to show that both are neotenic.

Conclusive evidence of the neotenic nature of *Xenopus* is offered by the structure of the V. *bulbi cordis posterior*, which, instead of entering the V. *abdominalis* as in *Rana*, flows direct into the sinus venosus (text-fig. 16). To quote Gaupp (1896, dritte Auflage, p. 412), who described the vascular system of *Rana*, "In frühen Entwicklungsstadien mündet, nach Goette, die V. *bulbi posterior* nach kurzem Verlaufe in den Sinus venosus. Ihre Verbindung mit der V. *abdominalis* und die Ueberleitung ihres Blutes in den Pfortaderkreislauf der Leber erfolgt secundär." (See also Escher, 1925.)

Two other unusual points in the veins of *Xenopus* deserve mention. Firstly, there is the complete absence of the V. *subscapularis* draining the arm, resulting in the absence of a V. *innominata*, since according to Gaupp the latter is formed by the junction of the V. *subscapularis* and the V. *jugularis interna*. Associated with this is the fact that the V. *dorsalis scapulae posterior* joins the V. *cutanea magna* instead of the V. *subscapularis* (text-fig. 4).

The second point of interest is that the V. *facialis* turns inwards with the A. *cutanea magna* to join the V. *capitis lateralis*, instead of continuing back over the arm to empty itself into the V. *cutanea magna* (text-fig. 4).

The reason for such variations is difficult to understand at first, but possibly some clue could be obtained from the embryology. These modifications are probably associated with the aquatic mode of life and the reduction in importance of the fore-limb under such conditions.

In the arterial system of *Xenopus* there are few points of particular

interest. The arteries as a whole conform well to the scheme given by Gaupp for *Rana*. It has already been noted by both Dreyer (1913) and Grobbelaar (1924) that the A. cutanea magna is not so well developed in *Xenopus* as in *Rana*, and that the reason can be found in the animal's mode of life in stagnant pools, which renders the skin of little use as a respiratory organ. This condition is carried still further in *Pipa*, where the A. cutanea magna is absent altogether (Grönberg and Klinckowström, 1893).

Other points of interest are the presence of the ramus muscularis of the A. carotis externa supplying the muscles of the ventral body-wall (text-fig. 2), and the fact that the A. occipito-vertebralis is given off as a branch of the A. subclavia and not from the aorta direct (text-fig. 3). The A. coeliaco-mesenterica resembles that of *Bufo vulgaris* in that it is given off from the median aorta abdominalis, and not from the left aorta thoracica as in *Rana* (Hafferl, 1933) (text-fig. 6).

Apart from the number of small variations which one might expect to find from one animal to the next, interesting abnormalities are often encountered. These appear to be particularly abundant in *Xenopus laevis*, for out of the 48 specimens dissected, 7 possessed major abnormalities. This gives an approximate 15 per cent. against O'Donoghue's figures for *Rana temporaria* (1931) which range from 0 to 5 per cent. In other species of *Rana* abnormalities are even rarer. Anatomical variations are admittedly common in the case of neotenic groups.

Besides these abnormalities there are certain variations which recur fairly regularly. A common one, found in approximately one-third of the animals examined, is the presence of an extra branch of the A. carotis interna, arising close to the origin of the A. cutanea magna and passing out with M. petrohyoideus to supply the floor of the mouth and the muscles attached to the outer posterior angle of the skull. The A. cutanea magna, too, often possesses additional branches to M. petrohyoideus, the oesophagus or the larynx.

SUMMARY.

1. The arterial and venous systems of *Xenopus laevis* (Daudin) are described in detail.
2. The main plan of the blood-vessels is similar to that of *Rana*.
3. The structure of the abdominal and hind-limb veins, however, and also of the V. jugularis externa resembles that of *Salamandra* more than that of *Rana*.
4. This resemblance is due to the fact that both animals are neotenic amphibian types.
5. The V. bulbi cordis posterior in *Xenopus* also has a larval (neotenic) pattern.

6. Other specialised points in the vascular anatomy are mentioned. Some of these are probably related to the exclusively aquatic habits of the animal; others are more difficult to explain.

7. *Xenopus* shows a higher percentage of variations and abnormalities than any of the commonly dissected species of *Rana*.

LIST OF ABBREVIATIONS.

MUSCLES.

Mm. abd. ind. l., abductor indicis longus; *add. mag. (c.d.)*, adductor magnus (caput dorsale); *add. mag. (c.v.)*, adductor magnus (caput ventrale); *anc.*, anconaeus; *anc. (c.l.)*, anconaeus (caput laterale); *anc. (c.m.)*, anconaeus (caput mediale); *anc. (c.s.)*, anconaeus (caput scapulare); *cocc.-il.*, coccygeo-iliacus; *com. cl.*, compressor cloacae; *cor.-brach. br.*, coraco-brachialis brevis; *cor.-brach. l.*, coraco-brachialis longus; *cor.-rad.*, coraco-radialis; *crur.*, cruralis; *cuc.*, cucullaris; *delt.*, deltoideus; *depr. mand.*, depressor mandibulae; *dors. scap.*, dorsalis scapulae; *epic.-cub.*, epicondylo-cubitalis; *epit.-cub.*, epitrochleo-cubitalis; *ext. carp. rad.*, extensor carpi radialis; *ext. carp. uln.*, extensor carpi ulnaris; *ext. cr. br.*, extensor cruris brevis; *ext. dig. com. l.*, extensor digitorum communis longus; *fl. ant. l. sup.*, flexor antibrachii lateralis superficialis; *fl. carp. rad.*, flexor carpi radialis; *fl. carp. uln.*, flexor carpi ulnaris; *gem.*, gemellus; *gen.*, genio-hyoideus; *glut. mag.*, glutaeus magnus; *grac. maj.*, gracilis major; *grac. min.*, gracilis minor; *ileo-fem.*, ileo-femorale; *ileo-fib.*, ileo-fibularis; *ileolumb.*, ileolumbaris; *il. ext.*, iliacus externus; *il. ext. (a.h.)*, iliacus externus (accessory head); *il. int.*, iliacus internus; *intercrur.*, intercruralis; *interscap.*, interscapularis; *lat. dors.*, latissimus dorsi; *lev. scap. inf.*, levator scapulae inferior; *lev. scap. sup.*, levator scapulae superior; *long. dors.*, longissimus dorsi; *mass. maj.*, masseter major; *obl. ext.*, obliquus externus; *palms. l.*, palmaris longus; *pectin.*, pectineus; *pect. (p. abd.)*, pectoralis (portio abdominalis); *pect. (p.st.)*, pectoralis (portio sterno-coracoidea); *per.*, peroneus; *petr.*, petrohyoideus; *plant. l.*, plantaris longus; *pter.*, pterygoideus; *pyr.*, pyriformis; *rect. abd.*, rectus abdominis; *rhomb. ant.*, rhomboideus anterior; *sart.-sem.*, sartorio-semi-tendinosus; *semin.*, semimembranosus; *serr. inf.*, serratus inferior; *serr. med.*, serratus medius; *serr. sup.*, serratus superior; *stern.*, sternohyoideus; *subh.*, subhyoideus; *subm.*, sub-maxillaris; *temp.*, temporalis; *ten. fas. lat.*, tensor fasciae latae; *tib. ant. br.*, tibialis anticus brevis; *tib. ant. l. (c.p.)*, tibialis anticus longus (caput peroneale); *tib. ant. l. (c.t.)*, tibialis anticus longus (caput tibiale); *tib. post.*, tibialis posticus; *trans.*, transversus.

ARTERIES.

Aa. brach., brachialis; *car. comm.*, carotis communis; *car. ext.*, carotis externa; *car. int.*, carotis interna; *cocc.*, coccygea; *coel.-mes.*, coeliaco-mesenterica; *cor.-clav.*, coraco-clavicularis; *cut. ant. l.*, cutanea antibrachii lateralis; *cut. fem. lat.*, cutanea femoris lateralis; *cut. fem. post.*, cutanea femoris posterior; *cut. mag.*, cutanea magna; *dors. scap. ant.*, dorsalis scapulae anterior; *dors. scap. post.*, dorsalis scapulae posterior; *epig.-musc.*, epigastro-muscularis; *fem.*, femoralis; *glut.*, glutaea; *hep.*, hepatica; *il. comm.*, iliaca communis; *int.*, interossea; *isch.*, ischiadica; *lumb.*, lumbalis; *mand. ext.*, mandibularis externa; *max. sup.*, maxillaris superior; *mes. post.*, mesenterica posterior; *occ.*, occipitalis; *occ.-vert.*, occipito-vertebralis; *oes.*, oesophagea; *ophth.*, ophthalmica; *orb.-nas.*, orbito-nasalis; *pal.*, palatina; *pect.*, pectoralis; *per. ant. sup.*,

peronea anterior superior; *popl.*, poplitea; *prof. br.*, profunda brachii; *prof. fem. ant.*, profunda femoris anterior; *prof. fem. post.*, profunda femoris posterior; *pulm.-cut.*, pulmo-cutanea; *pulm.*, pulmonalis; *rad.*, radialis; *r. musc.*, ramus muscularis; *spin. vent.*, spinalis ventralis; *subcl.*, subclavia; *temp.*, temporalis; *thor. abd.*, thoracica abdominalis; *thor. sup.*, thoracica superior; *urogen.*, urogenitalis; *vert. dors.*, vertebralis dorsii; *ves.*, vesicalis.

VEINS.

Fr. abdom., abdominalis; *abd. ant.*, abdominalis anterior; *abd. post.*, abdominalis posterior; *brach.*, brachialis; *bulb. cord. post.*, bulbi cordis posterior; *cap. lat.*, capitis lateralis; *caud.*, caudalis; *cava ant.*, cava anterior; *cava post.*, cava posterior; *cl. m.*, cloacae medialis; *cor.-clav.*, coraco-clavicularis; *corp. ad.*, corporis adiposi; *cut. fem. ant. med.*, cutanea femoris anterior medialis; *cut. fem. lat.*, cutanea femoris lateralis; *cut. fem. post. lat.*, cutanea femoris posterior lateralis; *cut. fem. post. med.*, cutanea femoris posterior medialis; *cut. mag.*, cutanea magna; *cut. max.*, cutanea maxillaris; *dors. ped.*, dorsalis pedis; *dor. scap. post.*, dorsalis scapulae posterior; *dors.-lumb. ant.*, dorso-lumbalis anterior; *dors.-lumb. post.*, dorso-lumbalis posterior; *epig. ant.*, epigastrica anterior; *fac.*, facialis; *fem.*, femoralis; *gas. ant.*, gastrica anterior; *gas.-duod.*, gastroduodenalis; *gas. med.*, gastrica media; *haem. post.*, haemorrhoidalis posterior; *hep.*, hepatica; *hep. dext.*, hepatica dextra; *hep. med.*, hepatica media; *hep. sin.*, hepatica sinistra; *il. ext.*, iliaca externa; *il. trans.*, iliaca transversa; *int.*, interossea; *isch.*, ischiadica; *Jac.*, Jacobsonii; *jug. ext.*, jugularis externa; *jug. int.*, jugularis interna; *mand. ext.*, mandibularis externa; *musc.*, muscularis; *musc. abd.*, muscularis abdominis; *musc.-thyr.*, muscularis-thyroidea; *oes.*, oesophaga; *ovar.*, ovarica; *ovid.*, oviducalis; *pect.*, pectoralis; *pect.-cor.-clav.*, pectoralis-coraco-clavicularis; *pel.*, pelvica; *peron.*, peronea; *popl.*, poplitea; *port. hep.*, portae hepatis; *pud.*, pudenda; *pulm.*, pulmonalis; *ren. rev.*, renalis revehens; *retr.*, retrosternalis; *subcl.*, subclavia; *vert.*, vertebralis; *vert. int. dors.*, vertebralis interna dorsalis; *ves. fel.*, vesica fellea; *ves.*, vesicalis; *ves. a.*, vesicalis anterior; *ves. p.*, vesicalis posterior.

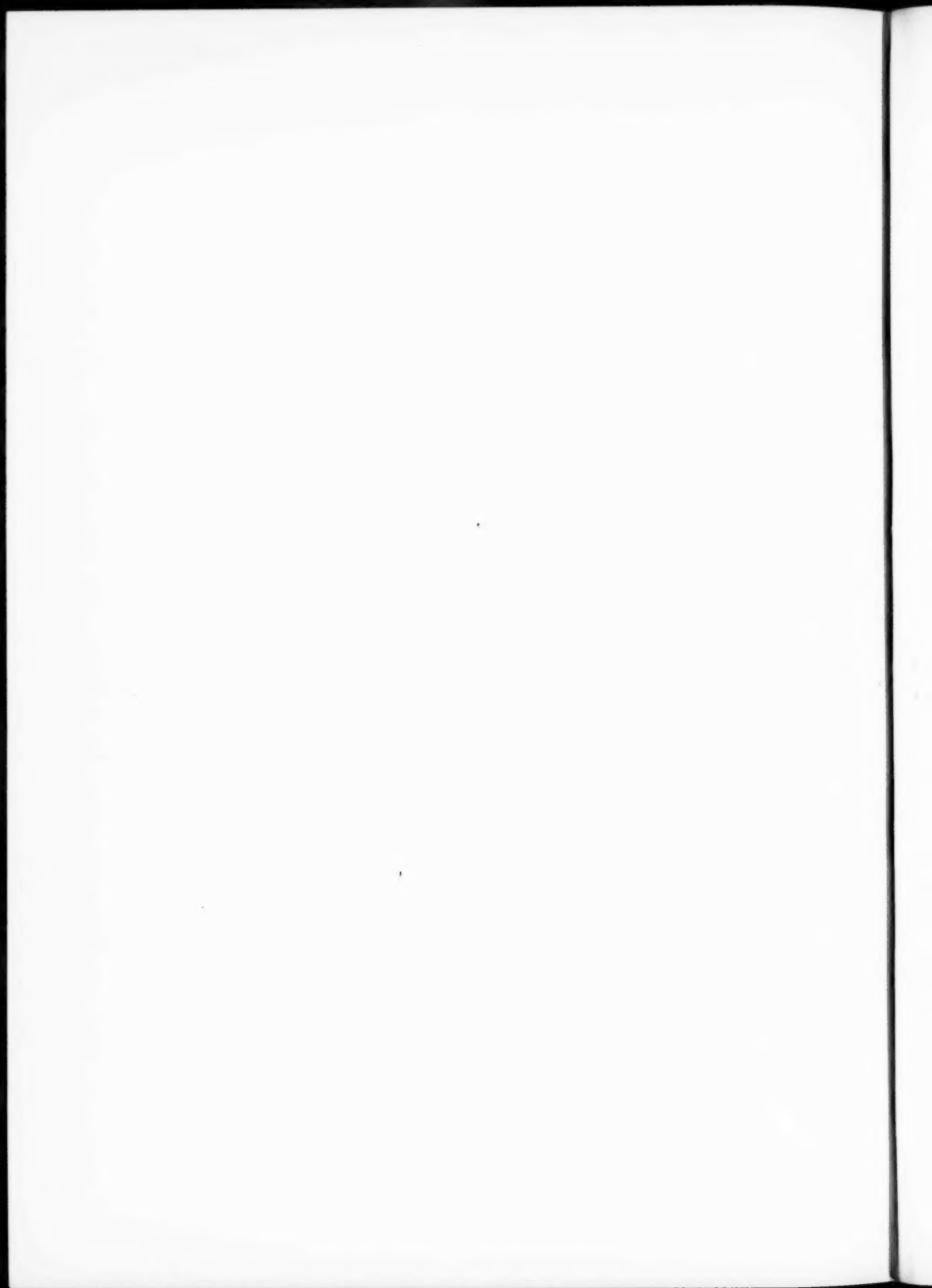
OTHER ABBREVIATIONS.

Ant. cornu., anterior cornu; *br.*, bronchus; *car. gl.*, carotid gland; *N. crur.*, Nervus cruralis; *N. isch.*, Nervus ischiadicus; *N. rad.*, Nervus radialis; *N. spin. II-X*, Nervi spinales II-X; *oes.*, oesophagus; *pl. br.*, plexus brachialis; *thyr. gl.*, thyroid gland.

REFERENCES.

1895. BEDDARD, F. E., "On the diaphragm and on the muscular anatomy of *Xenopus*, with remarks on its affinities," Proc. Zool. Soc. Lond., p. 841.
1913. DREYER, T. F., "The 'Plathander' (*Xenopus laevis*)," Trans. Roy. Soc. S. Afr., vol. iii, p. 341.
1914. —, "The morphology of the tadpole of *Xenopus laevis*," Trans. Roy. Soc. S. Afr., vol. iv, p. 241.
1925. ESCHER, K., "Das Verhalten der Seitenorgane der Wirbeltiere und ihrer Nerven beim Übergang zum Landleben," Acta Zool., Bd. vi, s. 307.
1934. FRANCIS, E. T. B., The Anatomy of the Salamander. Clarendon Press, Oxford.
1896. GAUPP, E., Ecker and Wiedersheim's Anatomie des Frosches. Bd. i and ii. Braunschweig.
1922. GILCHRIST, J. D. F., and VON BONDE, C., Practical Zoology for Medical and Junior Students. E. & S. Livingstone, Edinburgh.

1931. GREEN, T. L., "On the pelvis of the Anura: a study in adaptation and recapitulation," Proc. Zool. Soc., p. 1259.
1924. GROBBELAAR, C. S., "On the venous and arterial systems of the Platanna (*Xenopus laevis*, Daud.)," S. Afr. J. Sci., vol. xxi, p. 392.
- 1924 a. —, "Beiträge zu einer anatomischen Monographie von '*Xenopus laevis*' (Daud.)," Zeits. für Anat. u. Entw., Bd. lxxii, s. 131.
1893. GRÖNBERG, G., und KLINCKOWSTRÖM, A. v., "Zur Anatomie der *Pipa americana*. III. Gefäßsystem und subcutane Lymphsäcke," Zool. Jahrb., Bd. vii, s. 647.
1933. HAFFERL, A., und VAN GELDEREN, C., Arterien- und Venensystem der Amphibien. Handbuch d. vergl. Anat. d. Wirbeltiere, Bd. vi, ss. 563 und 685. Urban und Schwarzenberg, Berlin-Wien.
1933. JONES, E. J., "Observations on the pectoral musculature of Amphibia Salientia. A. The variability of the musculature in relation to the reduction of the clavicle, procoracoid and episternum," Ann. Mag. Nat. Hist., ser. 10, vol. xii, p. 403.
1933. KOTTHAUS, A., "Die Entwicklung des Primordial-Craniums von *Xenopus laevis* bis zur Metamorphose," Zeits. f. wiss. Zool., Abt. A., Bd. cxliv, s. 510.
1922. NOBLE, G. K., "The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification and phylogeny," Bull. Amer. Mus. Nat. Hist., vol. xlvi, p. 1.
1931. O'DONOGHUE, C. H., "Abnormalities in the blood vascular system of the Anura," Trans. Roy. Soc. Edin., vol. lvii, p. 179.
1939. PATERSON, N. F., "The head of *Xenopus laevis*," Quart. J. Mic. Sci., vol. lxxxi, p. 161.
1897. RIDGEWOOD, W. G., "On the structure and development of the hyobranchia, skeleton and larynx in *Xenopus* and *Pipa*; with remarks on the affinities of the Aglossa," J. Linn. Soc. Zool., vol. xxvi, p. 53.
1924. VILLIERS, C. G. S. DE, "On the anatomy of the breast-shoulder apparatus of *Xenopus*," Ann. Trans. Mus., vol. x, p. 197.
1929. —, "The comparative anatomy of the breast-shoulder apparatus of the three aglossal Anuran genera: *Xenopus*, *Pipa* and *Hymenochirus*," Ann. Trans. Mus., vol. xiii, p. 37.
1932. —, "Über das Gehörskelett der aglossen Anuren," Anat. Anz., Bd. lxxiv, nn. 4/5, p. 33.



THE GENUS *GYMNOCRANIUS* KLUNZINGER, WITH NOTES
ON CERTAIN RARE FISHES FROM PORTUGUESE EAST
AFRICA.

By J. L. B. SMITH.

(With Plate LVIII and one Text-figure.)

(Read August 21, 1940.)

During a revision of the South African Sparidae and Denticidae, I was able to examine two specimens of "*Dentex robinsoni*" Gilchrist and Thompson, on loan from the South African Museum. It was immediately obvious that the specimens were not congeneric with any other Denticid fishes in South Africa, and the species was placed in *Gymnocranius* Klunzinger. Since those borrowed specimens were not available for dissection, Barnard's diagnosis that they fell in the DENTICIDAE (i.e. *Dentex* Cuvier in the SPARIDAE *fide* Barnard) was provisionally accepted. Barnard had identified the specimens as *rivulatus* Rüppell, but since that name had been preoccupied (Bennett, 1835), a later synonym, *robinsoni* Gilchrist and Thompson, was accepted as valid.

During a recent visit to Portuguese East Africa a graduated series of specimens of "*Gymnocranius robinsoni*" was obtained, and a detailed study of those has led to an investigation extending far afield. In so far as the identity of the species is concerned, our specimens have erroneously been identified with *rivulatus* Rüppell, and are without question conspecific with the Indo-Pacific *griseus* Schlegel. Thus, since *robinsoni* Gilchrist and Thompson is shown to be a synonym of *griseus* Schlegel, and *rivulatus* Rüppell is invalid, it becomes necessary to rename that species, and *ruppellii* nom. nov. is now proposed.

Among the Perciformes there is a characteristic group of families which may be termed the Spariform fishes. These are characterised by the following: always 24 (10+14) vertebrae; emarginate, usually forked, caudal; moderate to small mouth, moderately protractile, with well-developed dentition; single dorsal with fairly strong spines, the spinous portion as a rule longer than the soft; the opercular bones not strongly spinate. These fishes are mostly littoral, few extending to deeper water, and they are found chiefly in the tropics, mostly in the Indo-Pacific. The families in this group are the SPARIDAE, the DENTICIDAE, the LUTIANIDAE, the LETHRINIDAE, and the NEMIPTERIDAE.

Dissection has shown that while *Gymnocranius* is undoubtedly Spariform (as here defined), and shows affinities with all the families, it cannot be placed in any of them, since it differs from any one by features of significance as great as those held to differentiate the existing families one from the other. Thus *Gymnocranius* cannot be placed in the SPARIDAE, DENTICIDAE, or NEMIPTERIDAE because of the structure of the maxillary bones, and of the reduced subocular shelf; nor in the LUTIANIDAE because of the nature of the subocular shelf, and because of the absence of palatal teeth, and of a supra-premaxillary process. From the LETHRINIDAE *Gymnocranius* differs in the nature of the subocular shelf, as well as in the structure of the maxillary bones, in the absence of transverse processes from the first two vertebrae, and by the sealing on the head.

A search for the nearest allies of *Gymnocranius* has revealed that several Spariform genera are indeed more closely related to *Gymnocranius* than to any genera in the families in which they have usually somewhat anomalously been placed, and that those genera with *Gymnocranius* form a structurally related group clearly differentiated from all other families of Spariform fishes.

The genera *Gnathodentex* Bleeker and *Pentapodus* Quoy and Gaimard certainly fall with *Gymnocranius*, and *Monotaxis* Bennett is also very closely related. These four genera contain small or moderate-sized carnivorous fishes, of similar habits and habitat, from the tropical Indo-Pacific. It is proposed that these receive distinction in the Spariformes by full family rank. Since *Pentapodus* Quoy and Gaimard is the oldest genus, the family is designated the PENTAPODIDAE.

It is immediately admitted that this diagnosis is venturesome in that I have been able to examine only one species of *Gymnocranius* and one of *Gnathodentex*, and that literature at my disposal is scanty. At the same time I have little hesitation in presenting the conclusions here set forth, since exhaustive analysis has pointed very clearly to them.

The taxonomic relationships of the families of the Spariformes and the clear distinction of the PENTAPODIDAE is shown by the following Key:—

Key to the families of the SPARIFORMES.

1. Subocular shelf strong, covering at least one-third of the subocular floor.
 - A. Premaxilla distally overlaps the lower edge of the maxilla.
No superior process on ramus of premaxilla internal to the maxilla.
 - x. Molars and/or incisiform teeth present . . . SPARIDAE.
 - y. Neither molars nor incisiform teeth present . . . DENTICIDAE.

- B. Premaxilla distally slips beneath maxilla. A superior process on premaxillary ramus which is internal to the maxilla.
- x.* Palate edentate NEMIPTERIDAE.
- y.* Some teeth on palate * LUTIANIDAE.
2. Subocular shelf feeble, at most a small triangular antrorse expansion from the second suborbital.
- A. Cheeks naked. Subocular shelf vestigial LETHRINIDAE.
- B. Cheeks scaly. Subocular shelf a triangular antrorse projection from the second suborbital PENTAPODIDAE.

FAMILY PENTAPODIDAE nov.

Body oblong-oval, fairly compressed. Head fairly broad, interorbital convex, prominent, prefrontals enlarge and form a preorbital prominence with age. Eye large. Nostrils both more or less circular.

Gill-rakers few, short, tubercular. Gill-membranes at most narrowly united, free from isthmus. Pyloric caeca few. Air-bladder notched posteriorly, with caudal horns. Dorsal spines 10, moderate, rays few. 3 anal spines. Caudal forked.

Mouth moderate or small, moderately protractile. Premaxillary rami shorter than pedicels, extremity internal to the maxilla, but without supero-posterior process behind the maxilla. Maxilla with broad posterior expansion. Anterior teeth conical, usually multiserial anteriorly, with a few antero-exterior enlarged, caniniform teeth. Laterally a single series of conical or molariform teeth. Palate and tongue edentate.

Subocular shelf small, in the form of a flat antrorse triangular projection from the upper anterior edge of the second suborbital, projecting within the first. Parietal and occipital crests well developed. Vertebrae 24 (10 + 14). Either all the vertebrae with parapophyses (*Gnathodentex*) or parapophyses from the third (*Gymnocranius*). The first rib sessile.

Scales moderate or large, feebly (to moderately) ctenoid. Head partly scaly. Interorbital naked or scaly. Cheeks scaly. Preopercle flange naked or scaly. Interopercle scaly only posteriorly. Dorsal and anal naked with low sheath, or with very low basal scaling posteriorly.

Key to the Genera.

1. Lateral teeth conical, sharp.
- Snout conical or at most moderately steep.
- A. All canines normal *Gymnocranius*.
- B. Lower canines flare outward.
- x.* Outer surface of maxilla smooth *Pentapodus*.
- y.* Maxilla with external denticulate ridge *Gnathodentex*.
2. Lateral teeth molariform. Snout very steep and abrupt *Monotaxis*.

* *Aphareus* Cuv. is generally placed in the LUTIANIDAE. Since it has an edentate palate and (11 + 13) vertebrae, investigation may show that it falls elsewhere.

Of the genera included, *Gymnocranius* Klunzinger has usually not been accepted as valid. Neither Regan (Ann. Mag. Nat. Hist. (8), vol. xii, 1913, pp. 111-145) nor Barnard (Ann. S.A. Mus., vol. xxi, 1927, p. 712) considered *Gymnocranius* worthy of consideration at full rank. Barnard placed the species in *Dentex* Cuvier, a diagnosis which has earlier been shown to be invalid (Smith, Trans. Roy. Soc. S.A., vol. xxvi, 1938, p. 291). Fowler (U.S. Nat. Mus. Bull., 100, vol. 12, 1933, p. 129) assigned *Gymnocranius* full rank in the SPARIDAE, but in his Key to Sparid genera characteristically defined *Gymnocranius* by an invalid feature. (See Smith, Trans. Roy. Soc. S.A., 1938, vol. xxvi, p. 227.)

Gnathodentex Bleeker has not been accepted by Fowler (*ibid.*, p. 69), who regarded it as a synonym of *Pentapodus* Quoy and Gaimard, but the genus appears worthy of maintenance, and is here accepted at full rank.

Genus GYMNOCRANIUS Klunzinger.

Smith, Trans. Roy. Soc. S.A., vol. xxvi, 1938, p. 291.

Body ovate, compressed. Eye large. Snout conical in juveniles, becomes steeper with age, with enlargement of the prefrontals.

Dorsal with 10 spines and 10-11 rays. A III, 9-10. All spines moderate. No fins greatly filamentous, first ventral ray sometimes extended. Caudal forked to lunate.

Scales feebly ctenoid, about 50 series. Cheeks with 4-5 series of scales. Interorbital and preopercle flange naked. Interopercle naked anteriorly. A naked groove in the scaling on each side of nape. Dorsal and anal with low basal scaling posteriorly.

Mouth small or moderate, jaws subequal. Villiform teeth in a band anteriorly in each jaw. A few antero-exterior enlarged teeth, normally caniniform. A single lateral row of sharp conical teeth. Premaxillary rami much shorter than pedicels, extremities slip beneath the maxilla.

Subocular shelf small, triangular, antrorse, from the anterior margin of the second suborbital, and internal to the first. Precaudal vertebrae with parapophyses from the third, the first rib sessile, but inserted behind the process so that it proximally lies against its posterior face.

Tropical Indo-Pacific fishes of moderate size, silvery to rose in colour in life. Generally six species have been accepted, though in 1933 Fowler (*loc. cit.*, p. 130) reduced the number to five, admitting *griseus* Schlegel, *microdon* Bleeker, *frenatus* Bleeker, *bitorquatus* Cockerell, and *robinsoni* Gilchrist and Thompson. I have seen only South African specimens from Natal and Portuguese East Africa, and they are all unquestionably referable to *griseus* Schlegel. Fortunately a regular series of graduated growth stadia has been secured, which shows clearly that this is a variable species,

and that changes occur with growth, chiefly in the form of the dorsal profile of the head. From the descriptions of *microdon* Bleeker available to me, my material shows that species almost certainly to be identical with *griseus* Schlegel. Also, one of my specimens which might well be identified as *frenatus* Bleeker is unquestionably conspecific with the remainder. Therefore, only three species in this genus, i.e. *griseus* Schlegel, *bitorquatus* Cockerell, and *ruppellii* nom. nov., are admitted here, and it would not be surprising if *ruppellii* eventually proves to be merely a colour variety of *griseus*: they differ in nothing else of significance. Between these three species admitted indeed the only feature of any significant differentiation is the coloration. At the same time, the three are in some degree expressions of geographical distribution, *griseus*, however, occurring throughout almost the whole Indo-Pacific.

Key to the species of Gymnocranius.

1. Wavy blue lines on snout and cheeks *ruppellii*.
2. No wavy blue lines on head.
 - A. Preorbital deeper than eye. A white loop in shoulder *bitorquatus*.
 - B. Preorbital not deeper than eye. Dark cross-bars; a bar through eye on cheek; a dark mark above pupil variably present . . . *griseus*.

Of the above, *bitorquatus* is known only from Australia, and is distinguished by a fairly deep preorbital, and by the white collar over the nape.

Gymnocranius griseus (Schlegel).

Gymnocranius griseus (Schlegel). Fowler, U.S. Nat. Mus. Bull., 100, 1933, vol. 12, p. 130.

Gymnocranius robinsoni (G. & T.). Smith, Trans. Roy. Soc. S.A., 1938, vol. xxvi, p. 291; Fowler, *loc. cit.*, p. 133 (part).

Dentex robinsoni Gilchrist and Thompson. Gilchrist and Thompson, Ann. S.A. Mus., vol. vi, p. 228, 1908; Barnard, Ann. S.A. Mus., vol. xxi, p. 712, 1927 (Natal).

Dentex rivulatus Ruppell. Gilchrist and Thompson, Ann. Durban Mus., vol. i, 1917, p. 356 (Natal).

Gymnocranius microdon (Bleeker). Fowler, *loc. cit.*, p. 132.

Gymnocranius frenatus (Bleeker). Fowler, *loc. cit.*, p. 133.

Body ovate, fairly compressed. Dorsal profile sloping gently in juveniles, with a slight supraorbital depression. With growth the profile becomes more abrupt, with the development of an antorbital prominence. The snout is subconical in juveniles and early adult stadia, more abrupt in adults. The nape is fairly sharp in juveniles, broadens somewhat with growth.

None of the opercular bones serrate, a moderate flat spine on opercle. The interorbital is only partly bony, the frontals being deeply concave above the eyes.

Depth 2.4-2.5, length of head 2.9-3.2 in length of body. Eye 2.9-3.1, snout 2.6-3.0, postorbital part of head 2.9-3.1, interorbital (total) 2.9-3.0, interorbital (bony) 3.5-3.6 in length of head. Lower margin of preorbital gently undulate, depth 1.4-1.7 in eye. Naked parts of head, *i.e.* snout, preorbital and interorbital, much pitted, spongy. Preopercle margin almost straight, broadly rounded at angle, outer margin with radiate fine ridges. Hind nostril circular. Pyloric caeca 2, one short, robust, the other longer, characteristically folded over the smaller.

On lower limb of anterior arch 5-6 gill-rakers, rudimentary spinate knobs. Gill membranes not united, free from isthmus.

Mouth terminal, moderate, very slightly oblique and only moderately protractile. Maxilla extends to below nostrils, almost below anterior margin of eye. The maxilla for the greatest part slips beneath the preorbital, but is distally exposed. With age the lips thicken considerably. In the lower jaw there is a patch of sharp curved villiform teeth closely adjacent on each side of the symphysis. Antero-exteriorly are usually 6 small to moderate canines, variable in size, position, and form, though the outer are generally the largest. Laterally, along the mandible, are on each side 6-9 fairly robust conical teeth in a single series. In the upper jaw the villiform teeth are in a band which is widest anteriorly, and which extends farther along the inner margin of the jaw, almost to the distal end of the pre-maxilla. There are usually 6 antero-exterior subequal caniniform teeth. Behind these, along the margin of the jaw, are on each side 5-7 fairly robust conical teeth. Palate and tongue edentate (text-fig. 1). Premaxillary pedicels 1.7 times rami.

D X, 9-10, inserted above behind hind margin of opercle. Base of spinous portion 3.3-3.4, of soft portion 4.9-5.2 in length of body. 1st spine 4.4-4.7, 2nd and 6th 3.0, 3rd 2.4-2.7, 4th 2.2-2.3 in head, remainder graduated shorter to the subequal 8th and 9th, 3.8-4.0 in head. Soft rays higher than last spine, 5th-7th longest, about 2.3 in head. Edge of soft fin gently and evenly convex. Pectorals 1.25-1.33 in head. Ventrals with first ray extended, 1.1-1.4 in head, reach to vent. Caudal almost lunate in juveniles, becomes less deeply incised in adults. Peduncle fairly slender.

Scales large, only feebly ctenoid. L.I. 47-50, l.tr. $\frac{6-7}{16-18}$, 4-5 series (usually 5) on cheek. 10-11 oblique rows predorsal. Lateral line tubes moderate, slightly oblique, without posterior pores. Predorsal scales

extend to above the hind margin of the orbit, sometimes a little farther forward in juveniles, but the interorbital is always naked. Preopercle flange naked. Only the hinder portion of the interopercle is scaly. Snout and chin naked. Hind portion of soft dorsal and anal scaly basally only.

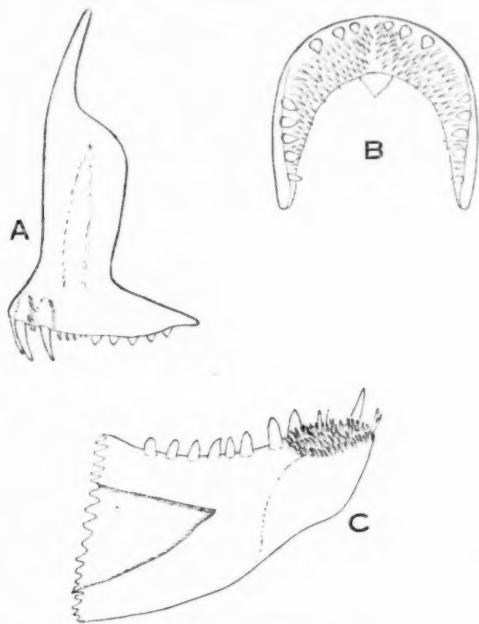


FIG. 1.—*Gymnocranius griseus* (Schlegel).

A. Side view of premaxilla. B. View of upper jaw from below. C. Dentary from within. Villiform teeth not accurately to size or number. All $\times 2$. From specimen 255 mm. in length.

Colour.—Juveniles, alive. Specimens up to about 180 mm. in length are silvery, slightly darker above, with few definite markings. As death approaches, 6–10 somewhat oblique narrow dark cross-bars, and numerous black spots, flash up spasmodically, and fade more slowly. The dark spots are more numerous on the caudal region. After death the dark markings slowly fade, most of the spots vanishing completely, while the cross-bars are of much diminished intensity.

Juveniles, preserved. The body is silvery-olive, lighter below. There are 8–10 narrow dusky cross-bars, the 1st from the interorbital through the eye across the cheek to the interopercle. The 2nd from the occiput

behind the orbit, in some cases continued to the chest. The 3rd runs from the nape, through the pectoral base, to the ventral origin, broadening, but becoming fainter below. The 4th runs backwards and downwards from the origin of the spinous dorsal, and fades below the lateral line. The 5th originates below the 5th-6th dorsal spines, and runs backwards and downwards, becoming fainter but fairly wide near the flank. The 6th originates with the soft dorsal, and runs backwards and downwards to the lateral line, where it turns gently forward and runs to the base of the anal spines: at each end it spreads over the membranes of the fins. The 7th is usually short and faint, originating below the last dorsal rays, and running forwards and downwards, fading out just below the lateral line. The 8th comes over the peduncle, and runs forwards and downwards to the middle of the anal. There are usually one or two variable bars or blotches on the hind part of the peduncle. There are 3-5 faint cross-bars on the caudal, medially very faint, appearing in some specimens merely as blotches along each lobe. All the main cross-bars are continuous dorsally, those on the nape markedly so. In some specimens there appears to be a dusky bar over the snout to the chin. Occasional dark spots, chiefly on the peduncle and caudal base.

Dusky scale centres form longitudinal lines of the scale rows, most noticeable on the flanks. Iris yellow-bronze. Membrane of spinous dorsal and anal dusky. Ventrals distally dusky. Caudal dusky. Pectoral, soft dorsal, and anal, light. Breast noticeably light.

Adults, preserved. Light olive or very light brown, lighter below. Markings are usually faint, but some or all of the bars described in the juveniles can quite clearly be traced. The bar across the cheek, with a dark blotch on the iris above, and the peduncular bar sloped forward and downward, are found in most specimens.

Length.—Up to 400 mm.

Locality.—Natal; Portuguese East Africa.

Distribution.—Indo-Pacific.

It is a peculiarity of this species that the eye remains of almost constant relative size, or even appears to increase slightly with age in some specimens. It is possible that this may be a result of environment, for while juveniles are commonly found in shallow water, adults are usually taken on lines in deeper water, though not at great depths where enlargement of the eye is commonly found.

Although rare in Natal waters, *griseus* is not at all uncommon farther north. At Lourenço Marques and Beira, specimens are usually to be found among the catches of the line-boats. In Delagoa Bay, about Inhaca Island, juveniles are frequently caught in fair numbers by nets. The species is conspicuous in the catch by the manner in which black cross-bars

and spots periodically blaze up and fade away on the silvery fishes. The fishermen had no particular name for this species.

This species appears to feed chiefly upon crustacea.

Gymnocranius ruppellii nom. nov.

Dentex rivulatus Rüppell (non Bennett). Rüppell, Neue Wirbelth. Fische, p. 116, pl. 29, fig. 2, 1835; Day, Fishes of India, 1875, p. 90.

Gymnocranius robinsoni (Gilchrist and Thompson). Fowler, U.S. Nat. Mus. Bull., 100, 1933, vol. 12, p. 133.

The species has been recorded from the Red Sea and from Ceylon. Fowler (*loc. cit.*, p. 134) includes a record by Pellegrin (Bull. Soc. Zool. France, vol. xxxix, p. 229, 1914) from Madagascar. I have not seen this record or description, so do not include it above.

There is little to distinguish this species from *griseus* Schlegel, save the blue markings on the head, and a doubtfully deeper preorbital. It has not yet been found in our region, though, if Pellegrin's record is valid, it doubtless occurs in the waters of Portuguese East Africa.

GENUS GNATHODENTEX Bleeker.

In all respects similar to *Gymnocranius* excepting: a shallower pre-orbital; a serrated external bony ridge on the maxilla; the lower outer canines flaring outwards; and the soft dorsal and anal entirely naked with low sheath. Brief examination shows how clearly *Gymnocranius* and *Gnathodentex* are related, and there is no doubt that they fall in the same family.

The genus is monotypic. The single Indo-Pacific species *aurolineatus* Lacepede was first recorded from South Africa (Delagoa Bay) in 1939 (Smith, Trans. Roy. Soc. S.A., 1939, vol. xxvii, p. 218).

GENUS PENTAPODUS Quoy and Gaimard.

Fowler, U.S. Nat. Mus. Bull., 100, 1933, vol. 12, p. 69.

Pentapodus differs from *Gnathodentex* Bleeker chiefly in the absence of the serrated maxillary ridge. A number of species from the Indo-Pacific have been described, and though I have seen no specimens, the general characters of the genus and the species leave no doubt that they fall with *Gymnocranius*. It appears likely that critical revision will divide the genus *Pentapodus* Quoy and Gaimard, as at present accepted, into at least two genera. This cannot be attempted without actual specimens, not at present available.

Genus *MONOTAXIS* Bennett.

Fowler, U.S. Nat. Mus. Bull., 100, 1933, vol. 12, p. 134.

This genus is closely related to *Gymnocranius* Klunzinger by the following characters in common: dorsal and anal fin formulae; few, knob-like gill-rakers; anterior dentition; fairly large scales, less than 50 series; naked interorbital and preopercle flange; few cheek scales; large eye; few pyloric caeca.

In the PENTAPODIDAE *Monotaxis* is clearly distinguished from all other genera by the lateral molar teeth, uniserial in each jaw, as well as by the very abrupt convex profile of the snout.

The single species *grandoculis* Forskål appears to be distributed throughout almost the whole of the tropical Indo-Pacific, and to occur abundantly at many places. It has been recorded from Madagascar. I could find no indication that the species had been seen in Portuguese East Africa, though I have little doubt that it should occur there.

FAMILY NEMIPTERIDAE.

Nemipterus delagoae nom. nov.

Nemipterus mulloides Smith, Trans. Roy. Soc. S.A., 1939, vol. xxvii, p. 129, fig. 2.

The new name is necessary since *mulloides* is invalid, having been preoccupied by *mulloides* Bleeker (1852).

FAMILY SERRANIDAE.

Variola louti (Forskål).

Day, Fishes of India, 1875, p. 26, pl. vii, fig. 3.

This handsome and unmistakable Serranid has been found to be an occasional capture in the waters off Delagoa Bay. Specimens up to 800 mm. in length were observed.

This species has not previously been recorded from South Africa, although reported from Zanzibar in 1866 (Playfair).

FAMILY PLATACIDAE.

Tripteronodon orbis Playfair.

Smith, Trans. Roy. Soc. S.A., 1935, vol. xxii, part iv, pp. 303-310.

This little-known species was first described in detail in the above paper. Even at that time comparatively few specimens were available, and the species was stated (p. 310) to be everywhere apparently rather scarce. The largest recorded size (Playfair) was 300 mm. It has subse-

quently been found that *T. orbis* occurs abundantly in the reefs in and about Delagoa Bay and on the coast of Portuguese East Africa. In certain localities the young are frequently taken in number by nets, while the adults are taken by lines from boats. The species attains the surprising size of over 20 lbs. in weight and 500 mm. in length. In these large, not uncommon, specimens the body is somewhat less deep and less orbicular than in the juveniles, while the 3rd to 5th dorsal spines are less elongate. Otherwise there is little change with growth.

FAMILY SCORPAENIDAE.

Amblyapistus binotata (Peters).

Amblyapistus marleyi Regan. Regan, Ann. Durb. Mus., 1919, vol. ii, part iv, p. 202, fig. 5; Barnard, Ann. S.A. Mus., 1927, vol. xxi, p. 917; Smith, Rec. Alb. Mus., 1931, vol. iv, part i, p. 156.

Barnard (*loc. cit.*, p. 918) called attention to the similarity between *binotata* Peters and *marleyi* Regan, but was not able to proceed farther in the absence of specimens. *Binotata* has been regarded as distinct from *marleyi* solely because the former was stated to have a round white spot on each side (hidden beneath the pectoral). *Binotata* is by no means uncommon in shallow water in and about Delagoa Bay, and the live fishes all have the white spot on the side, which, however, vanishes on preservation, when the specimens are indistinguishable from "*marleyi*."

The native fishermen would not handle this species, and stated that its spines inflict painful wounds.

FAMILY SYNANCHIDAE.

Synanceia verrucosa Bl. Schn.

Day, Fishes of India, 1878, p. 162, pl. xxxix, fig. 4.

This species was recorded from Zanzibar (without description) by Playfair (Fishes of Zanzibar, 1866, p. 49). Barnard (Ann. S.A. Mus., 1927, vol. xxi, p. 920) predicted that *S. horrida* (Linn.) would be discovered in our region. Recently it has been found that one species of *Synanceia* Bl. Schn. occurs in and about Delagoa Bay, thus probably throughout the waters of Portuguese East Africa.

According to Day's diagnoses (above) *verrucosa* and *horrida* are well differentiated from one another. The South African specimens agree closely in all respects with *verrucosa* Bl. Schn. as defined by Day. A single specimen from Delagoa Bay is described briefly below.

Head depressed, no saddle-shaped depression behind orbits, but a deep interorbital pit about as wide as eye. Body and fins with numerous

tuberculate excrescences. Gill-rakers merely low rudimentary spinate excrescences, 7 or 8 on the lower limb of the anterior arch. Apparently no slit behind the last gill. Two slender pyloric caeca. Stomach very thick and muscular. Teeth villiform, palate and tongue edentate.

D XIII, 7, the first three spines not markedly separate from the remainder, only the 2nd spine slightly higher than the 4th. A III, 5. P 19. Inner margin of ventrals adnate to body. Caudal rounded.

Colour dark brown, almost black, with an indefinite lighter wide cross-bar from over the middle of the spinous dorsal, another, fainter, from the soft dorsal. Extremities of spines and rays of dorsal, anal, pectoral and ventral light. Caudal light with a wide dark bar across the middle.

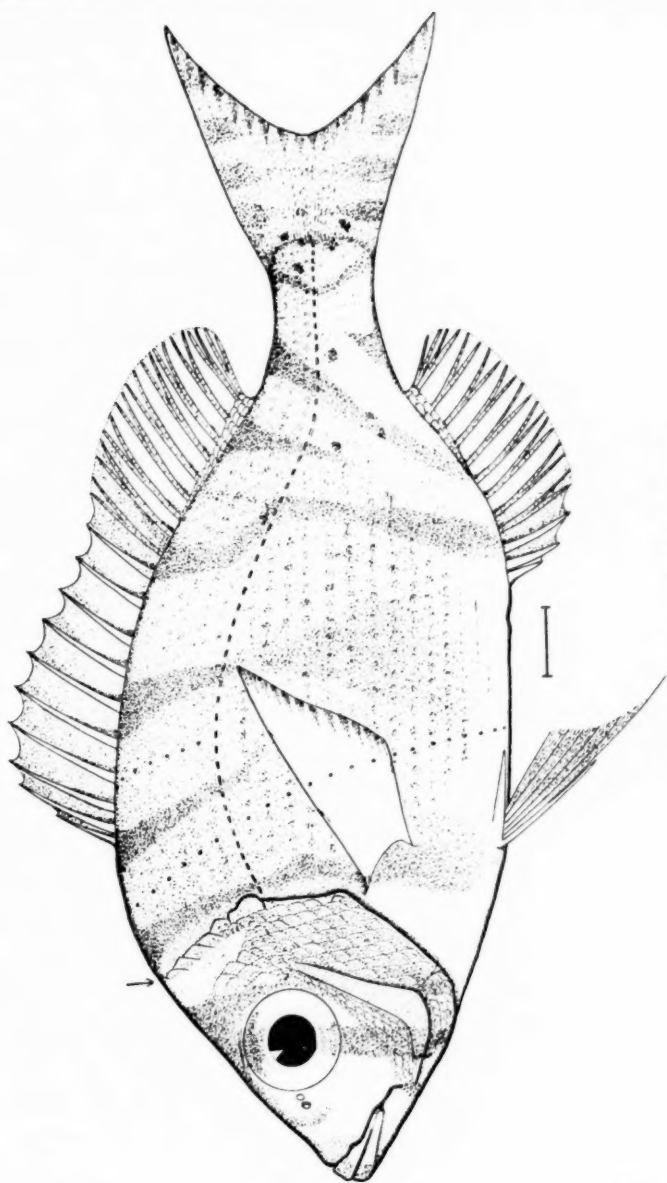
The specimen is an immature male, 130 mm. total length.

It is possible that *horrida* and *verrucosa* are sexual dimorphs, but material is not available to settle this point.

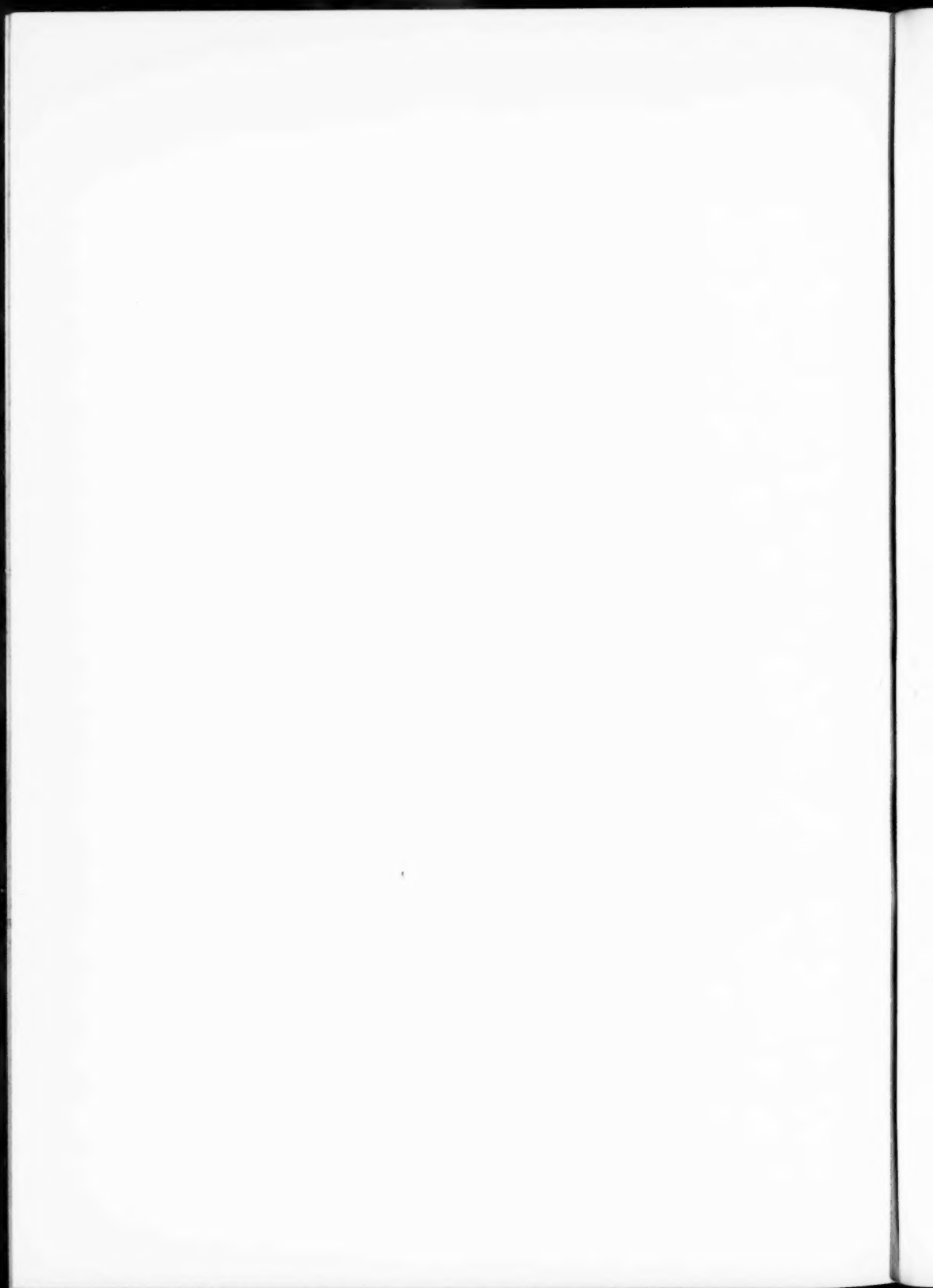
S. verrucosa occurs from the East Coast of Africa through the Indian Ocean (Day) to the Eastern Pacific (Fowler, Fish. Geo. Vand. S. Pac. Exp., 1938, p. 174).

I wish to express my gratitude to the National Research Board of South Africa for financial assistance which has defrayed part of the cost of the investigation.

ALBANY MUSEUM,
GRAHAMSTOWN,
July 1940.



Gymnochromis griseus (Schlegel). Juvenile.
The line represents 1 cm. The rows of large dots across the body represent scale rows.



SOME ECOLOGICAL FACTORS AFFECTING THE FERTILITY OF
TROUT EGGS AT THE JONKERSHOEK TROUT HATCHERY.

By D. HEY, M.Sc.

(Communicated by A. J. H. GOODWIN.)

(With one Text-figure, eight Graphs, and one Table.)

(Read September 18, 1940.)

INTRODUCTION.

The preliminary investigation of the low fertility of trout eggs at the Jonkershoek Trout Hatchery (Hey, 1939) indicated that none of the ecological factors investigated was adverse enough to have any marked effect upon the trout. Nevertheless, it is possible that the combined effect of a number of adverse conditions might lower the vitality of the fish, which in turn would affect the reproductive products. Consequently a detailed study of some of these ecological factors has been made. The data so obtained will serve as a basis for comparison with conditions prevailing at other institutions.

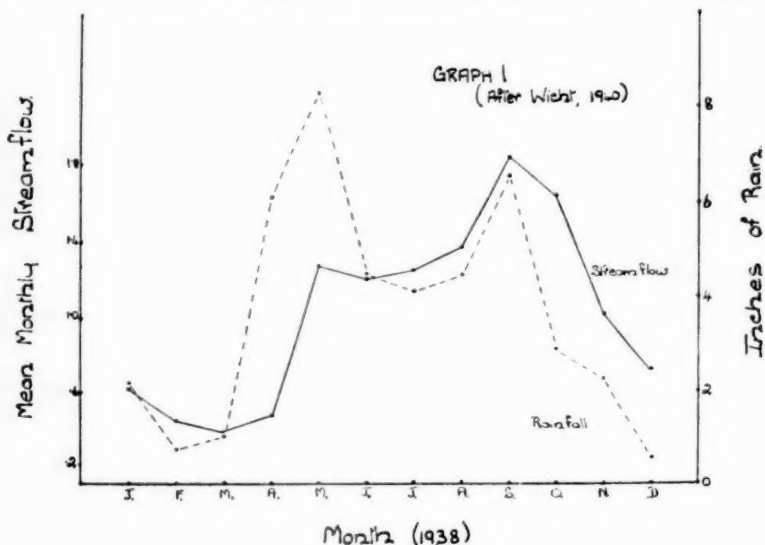
The Trout Hatchery is situated in the Jonkershoek Forest Reserve, about six miles from Stellenbosch (lat. $38^{\circ}58'$, long. $18^{\circ}57'$). The Reserve comprises the end of a long narrow valley which has been eroded along a line of faulting by the Eerste River. The valley runs in a north-west to south-east direction, and is enclosed by high mountains to the north-east, south-east, and south-west. The mountain-tops consist of bare Table Mountain Sandstone and are between four and five thousand feet high. The lower slopes are composed of T.M.S. talus overlying granite or Fransch Hoek shales. The slopes are covered with typical proteaceous shrub-vegetation, except where small forest remnants still exist along the stream beds. The soil is acid because there is no limestone in this area.

STREAMFLOW.

The most important requirement of any trout hatchery is an adequate supply of cool, clear water. The Jonkershoek Hatchery is supplied by a mountain stream from Bosboukloof, a tributary of the Eerste River. The stream is about two miles long and the catchment area is 514 acres. For the greater part of its course the bed of the stream is shaded by rank

matted vegetation, which tends to keep the water cool. The water appears crystal clear in the rapids, but is charged with fine black sediment.

The behaviour of this stream is being very carefully investigated by the Forest Research Officer, Jonkershoek, in connection with his forest-hydrological research. For this purpose a stream-gauging weir has been constructed, and a self-registering water-level recorder installed. I am



greatly indebted to the Forest Research Officer for placing his data and unpublished manuscript at my disposal (Wicht, 1940).

The stream is adequate for a pond-fish station, but is inadequate for successful trout culture in the hot, dry summer months when the flow is at its lowest. In order to give an idea of the behaviour of the stream throughout the year, the mean monthly streamflow was plotted against the rainfall. Graph 1 is taken from Wicht (*op. cit.*) and shows that there is a very large fluctuation in streamflow, the variation being .37 cu./secs. in March and 1.83 cu./secs. in September. This fluctuation is associated with rainfall. As can be seen, the flow in February was .44 cu./secs., March .37 cu./secs., and April .48 cu./secs., which can hardly be considered sufficient for intensive trout culture such as practised in Jonkershoek. The great disadvantage of a low streamflow in a hot climate is that it causes the temperature of the water in the ponds to rise.

The low summer streamflow is further aggravated by a daily fluctuation

in flow, the streamflow dropping to .18 cu./secs. at times. This has been investigated by Wicht, who has definitely established that during the hot summer months when no rain falls a daily fluctuation in streamflow occurs, such fluctuation being associated with hot weather. In graph 2 the streamflow in cu./secs. has been plotted every hour during a period when no rain fell. The data obtained from the water-level recorder chart were expressed in terms of streamflow, and the curves were rounded-off in accordance with this chart. The daily fluctuation is considerable, and the time taken by the stream to fall away is greater than the time taken to recover. A serious reduction in water-supply thus occurs when the air and water temperatures are high, leaving the stream with a flow of about .2 cu./secs., which is hardly adequate for trout culture.

This interesting fluctuation was made the subject of a special investigation by Wicht (*op. cit.*), assisted by the author. The evaporating power of the atmosphere over twenty-four hour intervals was measured by means of Livingstone-Thone atmometers. Three such atmometers were used and were weighed every twenty-four hours. After a correction factor had been applied, the mean of the three readings was calculated. The figure thus obtained is relatively accurate. In graph 3 the evaporativity of the atmosphere has been plotted against the amount of water lost to the stream in gallons every twenty-four hours. As the latter

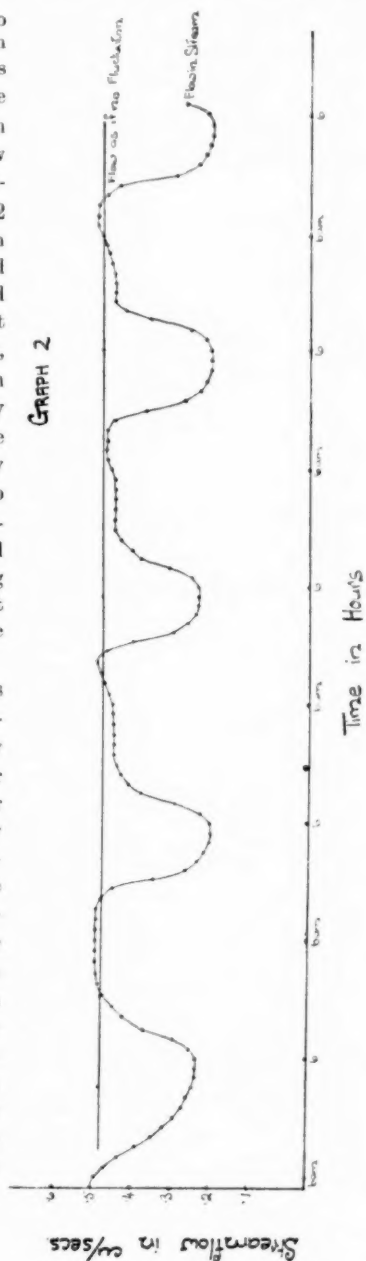
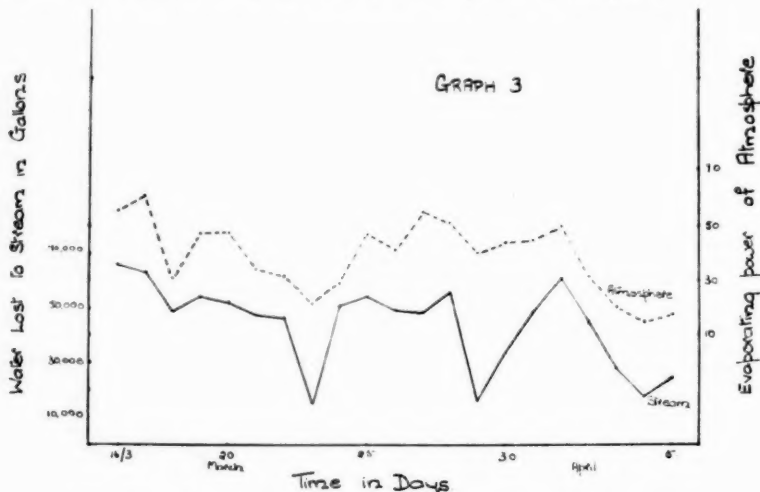


figure is very large, the graph is only relatively accurate. As can be seen, a fair correlation exists, and it therefore seems probable that the fluctuation is due to a large extent, if not entirely, to evaporation. Wind readings were also taken, but no correlation appears to exist. An investigation of the effects of the transpiration of plants in the stream bed upon the streamflow would be beyond the scope of the present investigation.



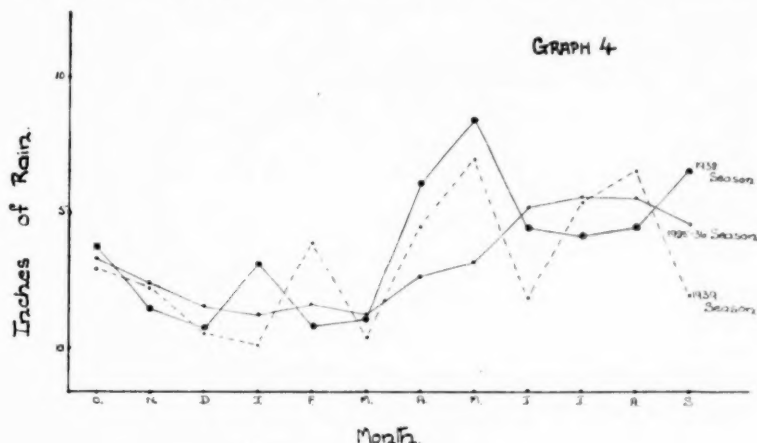
The Hatchery is entirely dependent upon the Bosboukloof stream, and consequently the amount of water available for use is limited by the flow in that stream. It is unfortunate that more attention was not paid to these details when the site for the Hatchery was chosen. Had it been on the Eerste River an unlimited water-supply would have been available. The Bosboukloof stream, although sufficient to support the Hatchery, can by no means be regarded as "an abundant supply of pure water," as stated by Wardlaw Thompson (1913).

RAINFALL.

The region enjoys a humid, temperate, winter-rainfall climate. The prevailing wind which carries the rain blows from the north-west directly into the Jonkershoek valley. A detailed analysis of rainfall in Jonkershoek has been carried out by Wicht (1939).

The nature and distribution of the rain influences the spawning season, which usually lasts from the end of May to the beginning of September. The year—as far as trout culture is concerned—thus extends from October

of one year to September of the next. Heavy rains at the beginning of such a year ensure an adequate streamflow throughout the summer months, and this has a beneficial effect upon the fish. Heavy rains at the end of such a year induce the fish to spawn earlier than usual. In graph 4 the monthly rainfall during the 1938 and 1939 cycles as registered by the Forestry gauge No. 11, situated in the middle of the Bosboukloof

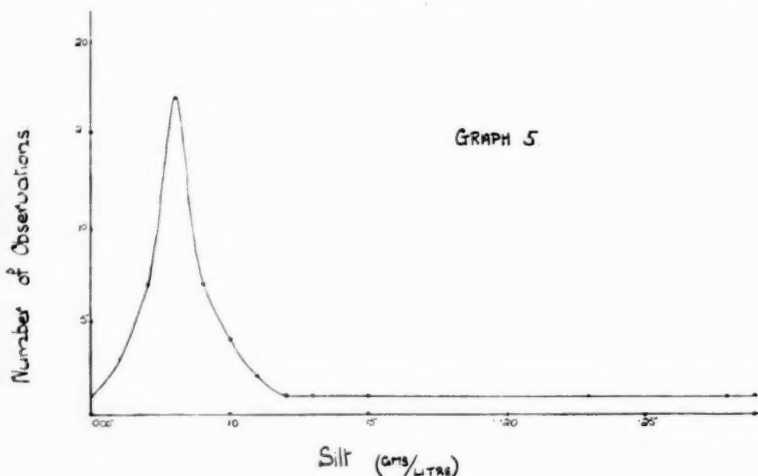


stream catchment area, is compared with the mean monthly rainfall during the years 1925-1936 as registered by the Meteorological Office gauge (Reports of the Chief Meteorologist, 1925). The greatest precipitation occurs in the months May to October. During the months November to March very little rain falls and the air temperature is high. As the streamflow is low and the water temperature high, the fish become listless and show no desire to feed. Were the rains spread more evenly over the year, the climate would be more suitable for trout culture. Even during the winter the rain is scattered and periods of heavy precipitation alternate with long dry spells. The longest of these dry spells during the 1939 season was from the 20th May to the 9th June, and periods of five days and over were frequent. During these dry spells of sunny weather the trout do not ascend the raceways to spawn, and consequently the eggs tend to overripen. Furthermore, the stream is "flashy," each shower causing a steep spate. These steep spates are due mainly to the precipitous nature of the catchment area and the showery nature of the rain. Were the rainfall distributed more evenly over the year, more constant streamflow would no doubt result. If the Hatchery were supplied by a larger stream

of water it would be independent of the rainfall, as the flow at the inlet could then be regulated. The volume delivered by this stream should be so large that at no time of the year would the total flow be used.

SILT.

The Bosboukloof stream, although apparently clear, carries silt in suspension. This silt has three detrimental effects upon the Hatchery:



1. The water used in the hatching house has to be filtered. 2. It smothers the aquatic vegetation, and consequently only the hardiest plants survive. 3. A large amount of silt is deposited in the ponds annually. The removal of this silt involves a considerable amount of labour.

The silt was analysed by the Department of Agricultural Chemistry of the Stellenbosch Elsenburg Agricultural College and was found to consist of: Organic matter, 39.87 per cent.; very fine sand, 51.1 per cent.; Fe_2O_3 , 6.8 per cent.; other constituents, 2.23 per cent. The opinion had been expressed that this silt is composed chiefly of diatoms. Consequently twenty random samples were examined microscopically, and although diatoms were present they were far from numerous.

The water was analysed quantitatively at intervals over a year to determine the total solids in suspension. In all fifty determinations were made in duplicate. The method employed was simple although lengthy (Standard Methods of Water Analysis, 1933). One litre samples were taken in duplicate, filtered through Gooch crucibles and dried at $103^\circ\text{--}105^\circ\text{C}$.

For the greater part of the year the water contained .008 gram of silt per litre, with .005 and .362 as the variation, although readings as high as .362 were only obtained at the apex of a heavy spate. Although some correlation must exist between the amount of silt in suspension and the rainfall, time of sampling, streamflow, volume of spate, etc., no such correlation could be found. This is probably due to the fact that only fifty determinations were made. Graph 5 is a frequency distribution curve. This curve represents fairly accurately the conditions existing in the stream. Except where a few samples were taken as near the apex of a spate as possible, the sampling was random.

By the construction of a series of settling tanks it would be possible to eliminate the greater part of this silt. This, however, would be an expensive undertaking.

TEMPERATURE.

A record of the water temperatures at the inlet and outlet to the Hatchery was obtained from self-registering maximum and minimum thermometers placed about 4 cm. below the surface of the water. In graph 6, the mean monthly maximum and minimum temperatures at both these points is represented. From this graph it is obvious that there is a very marked annual fluctuation in temperature. This is most noticeable in the large stock pond (outlet), where the variation is as much as 12.09°C . in a year. Furthermore, the water temperature is much higher than that tolerated by trout under natural conditions. According to Creaser (1930), "the maximum temperature for natural, self-sustaining, brook trout waters is now well established at about 19°C ." For six months of the year the maximum temperature in the stock pond is above this figure. Even the minimum temperature is higher than this for three months. As the European Brown Trout is not as hardy as the American Brook Trout, their toleration limit would be even lower.

The lethal temperature for Brown Trout, according to the research of Embury (1921), is about 30°C . Although at times the water temperature in the stock pond approaches this figure, the mean is well below it. It therefore appears that the trout at the Hatchery are living in water well above the optimum yet below the lethal temperature. Where we have fish kept year after year under these conditions, is it surprising that the ova produced are not of the same standard as those produced in a cold country?

Fish are said to react to very small differences in temperature. Krogh (1914) found that the rate of metabolism of a fish is uniformly raised or lowered with a rise or fall in temperature. Therefore trout at Jonkershoek require more food than they would in a colder climate. Unfortunately

the Curator has always found that heavy feeding during the summer results in a correspondingly heavy mortality. In consequence the condition of the stock fish remains poor throughout the summer. It is only during the month of April that the fish can be fed heavily. In May the feeding is again reduced owing to the proximity of the stripping season, as overfeeding at this time is supposed to cause degeneration of the eggs (Benecke, 1902).

An investigation of the effect of diet upon the trout will be dealt with in a further paper. The combined effect of a natural diet and cooler water on Brown Trout was, however, examined. Four hens and three cocks, varying in age from three to five years, were placed in the pond nearest the inlet, where the water is a few degrees cooler than in the stock pond. Here they were kept from October 1939 until April 1940. During this period the mean monthly minimum and maximum temperatures were 15.3° C. and 20.2° C. respectively as compared with 18.1° C. and 23.0° C. in the stock pond.

The stock fish were fed on the regular diet of minced liver, heart, salmon-roe meal, and fish biscuit. The fish in the experimental pond were fed heavily throughout the duration of the experiment on live food such as tadpoles, small crabs, minnows, and snails. These fish produced 3290 eggs (820 per fish), having a mean percentage fertility of 94.5. Eleven stock fish of approximately the same weight and stripped at the same time gave 7247 eggs, with a mean percentage fertility of 81.3. The experimental fish therefore showed an improvement of 13.2 per cent. in fertility. The improvement is more apparent when we compare the percentage of well-developed embryos. In the case of the experimental fish this was 92.4 as compared with 67.4, a difference of 25 per cent. These experimental eggs were also superior in size and colour to those produced by the stock fish. The mean diameter of the former was 5.5 mm. as compared with 5.0 mm. in the case of the latter. This improvement in size is due undoubtedly to the diet, and is in accordance with the findings of Stratton Gerrish (1940), who states that "the general result of a good season is to produce large eggs and many eggs in the next spawning season but one."

Although it is realised that these data are an inadequate basis for any definite conclusions, yet they are adequate to show that the quality of the eggs might be improved by the combined effects of cooler water and a more natural diet. This hypothesis could only be proved by repeating the experiment on a large scale.

Although the control batches of eggs constituted the first strippings (which have already been proved to be the best (Hey, 1940)) of eleven hens, yet in no single case was the fertility above that of the experimental

batches. The very low percentage of deformed and weakly developed embryos is also highly significant.

As the temperature of the water appeared to be such an important factor, it was investigated further in the stock pond. This pond is 34 metres long, 18 metres wide, and 2.5 metres deep. The daily fluctuation in water temperature at different depths was observed with a dual-terminal Casella temperature recorder. The first set of readings were obtained with the lower terminal 15 cm. from the bottom of the pond, and the upper 5 cm. below the surface of the water. A record of the air temperatures and wind during this period was obtained through the courtesy of the Forestry Department. By lowering the upper thermometer 25 cm. each week, a record of the temperatures at different levels in the pond was obtained. The results of this experiment may be summed up as follows: 1. At the surface the temperature fluctuated as much as 7.75°C . daily, the fluctuation decreasing with depth. The greatest fluctuation in the lower temperature was only 2°C . 2. The maximum difference between the bottom and surface temperatures was 7°C ., whereas the minimum was only 1°C . 3. There is a time lag of two hours between the surface and bottom temperatures. 4. The water takes about eight hours to heat up and sixteen to cool down again. 5. According to Smolian (1920) and Creaser (*op. cit.*), 19°C . may be regarded as the optimum temperature for Brown Trout. As the surface temperatures recorded are well above the optimum, one would expect the fish to inhabit the cooler water at the bottom of the pond. Here the average temperature recorded over eleven days was 21.56°C ., which is also well above the optimum. 6. At all depths a correlation between air and water temperatures was observable.

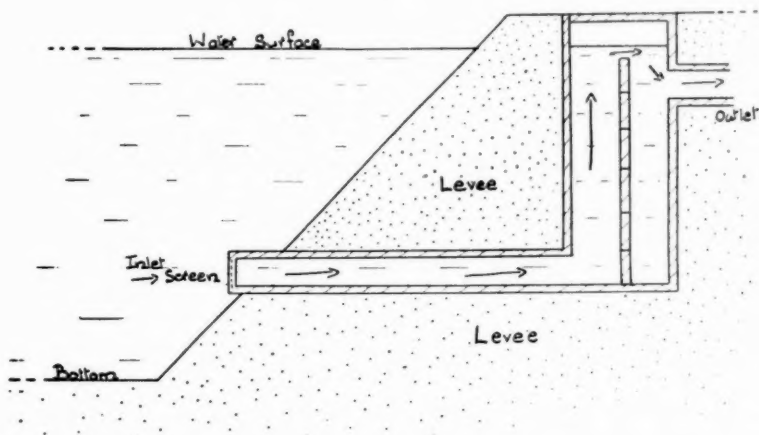
As a result of this experiment it may be definitely concluded that the water temperature in the stock pond is above the optimum for trout culture. There is a gradual drop in temperature from the surface to the bottom, and there is no stratification (Needham and Lloyd, 1916). There is a close correlation between the air and water temperatures, which is affected to some extent by the wind.

CONCLUSIONS.

There is a daily fluctuation in the temperature of the water-supply to the Hatchery. This water runs in an open furrow from the Forestry stream-gauging pool, and is consequently exposed to the sun. By means of self-registering maximum and minimum thermometers placed in the above-mentioned pool and in the intake pond at the Hatchery, it was found that there was a difference of 3°C . in the maximum and 1.7°C . in the minimum temperature at these two points. This rise in temperature

might be eliminated as follows: A concrete inlet reservoir approximately $5 \times 2 \times 2$ metres should be constructed just below the gauging weir. From here a 30-cm. pipe, buried well below the surface of the soil, would carry the water a distance of 180 metres to the settling pond. As has already been shown, the water at the surface of a large pond is considerably warmer than that near the bottom. The present outlet to the settling

FIG. 1



Outlet: (Adapted from Kteuz, 1928)

pond is so constructed that this warmer surface water is drawn off. By the use of a special outlet, as suggested in fig. 1, the colder water from near the bottom of the pond could be utilised. From this outlet the water would be carried by pipe to a pond, approximately three metres deep and sufficiently large to accommodate all the stock fish. This should be shaded by a canopy of wooden slats to reduce surface heating of the water, at the same time allowing sufficient sunlight to filter through. Were these improvements effected, it is highly improbable that the temperature of the water near the bottom of the pond would ever be above 19°C . This cooler water would undoubtedly have a beneficial effect upon the trout, and if to this were added a natural diet such as that used in the experiment described above, there seems no reason why the fertility of the eggs could not be raised.

Acidity of the Water.

The Bosboukloof stream is about two miles long and is fed by numerous side streams. The flow to the Hatchery is about .4 cu./secs. The water issues from the junction of the T.M.S. and the granite. (The lower shale of the T.M.S. is absent in part of this area.) The stream flows over granite and the T.M.S. talus forms the stream load. The impurities in the water are all derived from the granite or T.M.S. alluvium. The sandy deposit of silt, as also the acidity of the water, is probably due to the T.M.S.

The acidity of a natural water may be due either to the chemical composition of that water or to the effects of the fauna and flora in it. In the latter case the acidity would be caused by the dissolved carbon dioxide produced during respiration. In order to prove whether or not the acidity at Jonkershoek was due partly or entirely to dissolved carbon dioxide, triplicate samples of water from the inlet and the outlet were tested as follows: The pH of the samples was measured. They were then heated to the boiling-point to expel all dissolved gases. After cooling, the pH was again measured. The results are given in Table I, from which

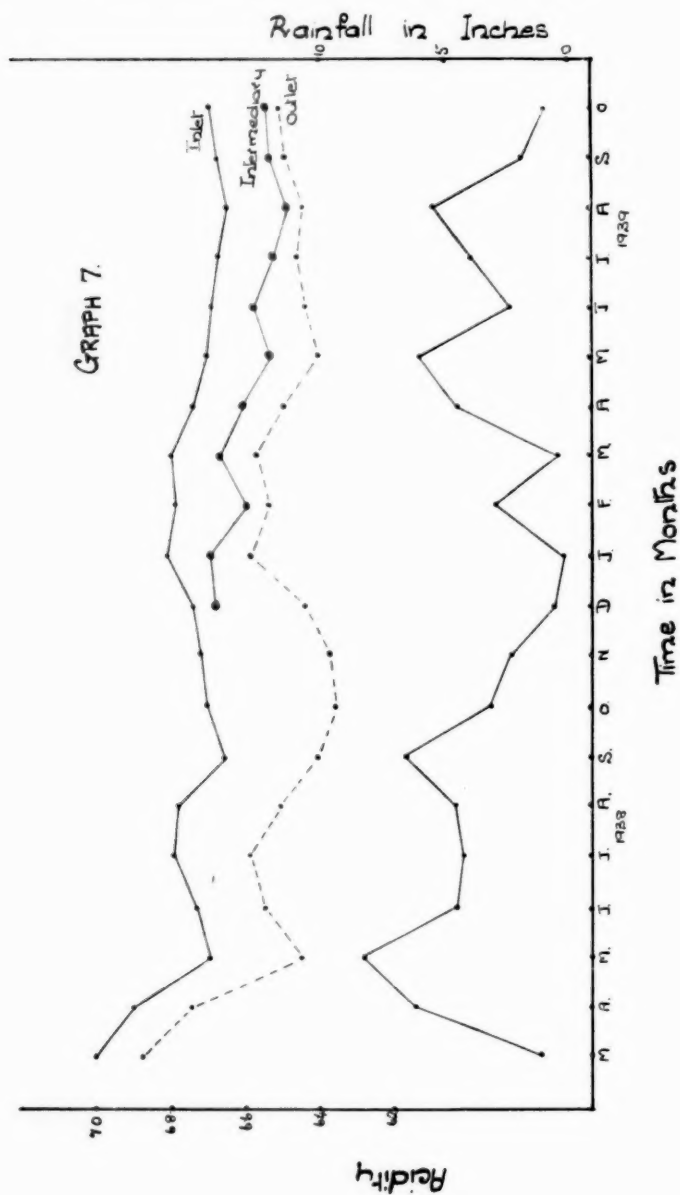
TABLE I.

Date.	Inlet.			Outlet.		
	Sample.	pH before Boiling.	pH after Boiling.	Sample.	pH before Boiling.	pH after Boiling.
9/1/40	A	6.9	7.0	<i>a</i>	6.6	6.9
	B	6.9	7.0	<i>b</i>	6.6	7.0
	C	6.9	7.0	<i>c</i>	6.6	7.0
	D	6.9	7.1	<i>d</i>	6.6	7.0
	E	6.9	7.0	<i>e</i>	6.6	7.1
23/1/40	A	6.8	7.0	<i>a</i>	6.4	6.9
	B	6.8	7.0	<i>b</i>	6.4	7.0
	C	6.8	7.0	<i>c</i>	6.4	7.0
	D	6.8	7.1	<i>d</i>	6.4	7.0
	E	6.8	7.0	<i>e</i>	6.4	7.0

it is evident that the acidity, especially in the case of the outlet, is due to dissolved carbon dioxide. The normal balance between the free atmospheric carbon dioxide and the amount dissolved in water is about pH 6.8. The acidity of the water at the inlet is therefore due to dissolved atmospheric carbon dioxide, whereas that at the outlet is due partly to carbon dioxide produced by the aquatic vegetation and fish. Southern (1932),

working on acid waters, has also found that water from non-limestone rocks normally has a pH range of 4.0 to 6.8.

Determinations of the acidity at the inlet, outlet, and an intermediary pond were made three times a week over a period of twenty months. From these results the mean monthly pH was calculated. In graph 7 this is compared with the rainfall. The graph shows that the acidity rises as the water flows through the ponds. According to Cowles and Schwitalla (1923), "when water flows rapidly over a clean bed, most noticeably at falls and rapids, the pH is raised, probably as a result of aeration." It is therefore possible that this rise might be prevented by a more efficient system of aeration at the Hatchery. The graph shows further that there is a very definite correlation between the acidity of the water and the rainfall. This is due to the fact that rain increases the pH by lowering the buffer action of the water. Richmond (1927) states: "Acidity varies with rainfall and other circumstances, and that its deadliness to trout varies with the temperature. It usually rises to its highest point during floods, and the higher the water temperature the more deadly it is." Never at any time, however, does the Bosboukloof stream drop below pH 6.2, which is well within the safety zone. Furthermore, the rain falls in winter when the water is at its coldest. According to Richmond (*op. cit.*), "the European Salmonidae are more sensitive to acidity than either of the two American species, *Salmo fontinalis* and the Rainbow Trout." As shown in a previous paper (Hey, *op. cit.*), the fertility of Brown Trout is lower than that of the Rainbow Trout, and it is possible that the acidity of the water may be a contributory cause. It was further observed that there is an annual fluctuation in acidity. The water is least acid between January and March, after which the acidity rises, reaching its maximum in August. This fluctuation is correlated with the annual fluctuation in rainfall. Where, as in Jonkershoek, the ponds contain aquatic vegetation, there is the possibility of a daily fluctuation in pH resulting from photosynthesis. This fluctuation would be dependent upon factors such as intensity and duration of sunlight, etc. Philip (1927), investigating hydrogen ion activity in a Minnesota lake, found that "a series of stations showed decided variations in pH values on the same day, especially over the shallower vegetated portions." In a large volume of water containing only a few organisms (fish and plants) the variations in pH may be too slight to detect. On the other hand, if a large number of organisms are present in a small pond, and as carbon dioxide is a factor in determining pH, we should find a daily periodicity in the pH values. To investigate whether or not such a fluctuation did exist, four-hourly determinations of pH were made at the three stations already mentioned. The pH was measured with a Leeds and Northrup potentiometer, using a



quinhydrone electrode. From a standard conversion table, the voltage reading was converted into pH at the given temperature. The results of this experiment were negative in that a daily fluctuation in pH did not appear to exist. The fact that the water became more acid as it flowed through the ponds was, however, corroborated.

In conclusion it might be repeated that the Bosboukloof water is acid. This acidity, however, is not great enough to have any profound effect upon the fish. As Brown Trout are more sensitive to acid water than Rainbow, it may contribute in causing a lower fertility of Brown than Rainbow Trout eggs.

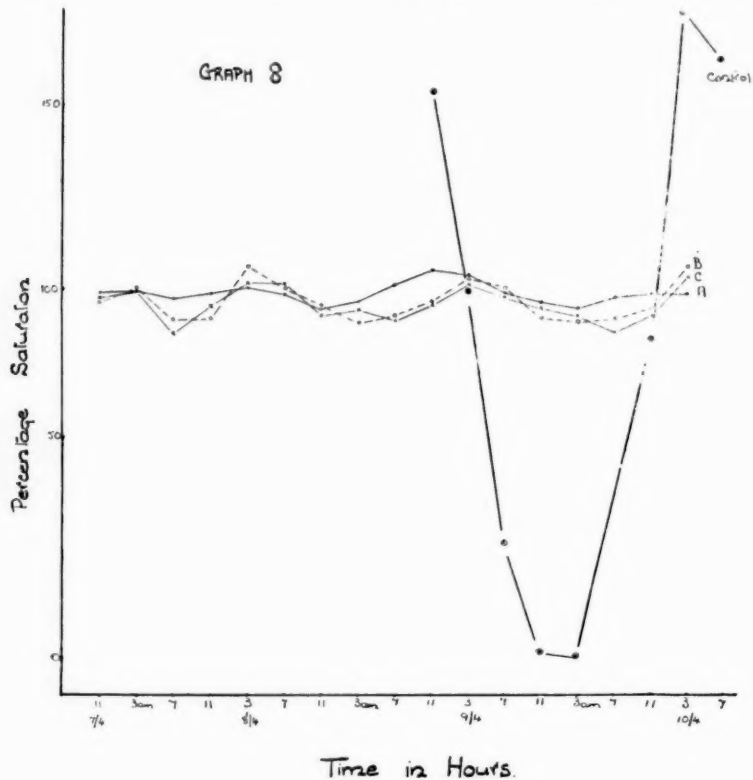
Oxygen Content of the Water.

The oxygen content of the Hatchery water-supply was determined bi-weekly over a period of four months. It was found that this varied between 91.9 and 99.5 per cent. saturation. That this is entirely satisfactory is confirmed by the work of Southgate (1933), who states: "Summarising the results of the experiments, it would appear that trout do not suffer from shortage of oxygen in water containing dissolved oxygen to the extent of not less than 50 per cent. of the saturation value."

In order to find out whether there was a daily fluctuation in the oxygen content of the water, determinations were made on samples of water from the same three stations as in the case of the pH tests. Duplicate samples were taken in each case and the oxygen content determined by the Winkler method. As a control, the oxygen content of the water in a small pond with a very rich plant growth, but containing no fish, was determined as above (Standard Methods of Water Analysis, 1933). The results are represented in graph 8. The temperature, which determines the relative oxygen solvent power of the water, was low at the time of sampling. The graph shows that the oxygen at all three stations was consistently high. That the oxygen content of the water is well above the danger line is shown by a comparison with the results of other workers. Gutsell (1929), quoting the work of Gardner and associates, on Brown Trout states: "The asphyxial condition in the case of trout was found to take place within narrow limits. At or below a certain point they died, slightly above they recovered—at 18° C. with 2.13 p.p.m., 24° C. with 2.81 p.p.m., and at 25° C. with 3.4 p.p.m." In corroboration Powers (1923) states: "All experiments that have been recorded in the literature indicate that a fish suffers very little or no ill effects by the reduction of the oxygen tension of untreated water, until the oxygen has been reduced to about 2.4 to 0.3 c.c. per litre, depending upon the species of fish."

The graph further shows that a slight daily fluctuation in oxygen content does occur. This is most apparent at station C, where the

maximum occurs at 3 p.m. and the minimum at approximately 3 a.m. This fluctuation is probably associated with the respiratory and photosynthetic activities of the plants. In the case of the control, this fluctuation is obviously due to the above-mentioned factors. In this case, however, we have a small volume of water in proportion to the aquatic growth.



Light.

Bissonnette (1932) has shown that light is a factor affecting natural reproduction. He found that the sexual activity in both males and females of many animals can be modified at will by altering the daily light ration. He has also found that not only the daily duration of light but also the wave-length and intensity conditions sexual activity in starlings.

Hoover (1937) has found that even in trout the sexual cycle can be modified by light. He selected a late spawning strain of fish and experi-

mentally exposed them to an artificial light cycle which was designated to simulate the total number of hours of sunlight to which fish were exposed during the average year at 44° latitude. "Starting on February the 20th, the daily light period was increased gradually, one hour per week, until eight hours of light were added to the normal daylight period. The light hours were then gradually decreased until the normal day was reached. On August the 12th all the experimental male fish were found to contain copious quantities of spermatozoa. The female fish were not quite ripe. The first eggs were taken from the female fish on August the 31st, which is approximately three months before the normal spawning time."

Unfortunately it has not been possible to investigate light in Jonkershoek. Here, however, it would be of advantage to retard instead of advance the spawning season. The shading of the stock pond, as suggested in the section on temperature, might have the added advantage of retarding spawning. By reducing the light in this manner the fish might be induced to spawn later.

FINAL CONCLUSIONS.

As a result of this investigation it appears that the low fertility of the eggs is due to a combination of three factors: 1. An unsuitable stripping technique (Hey, *op. cit.*). 2. High water temperature. 3. An inferior diet.

The first two factors have been investigated thoroughly. By applying the results obtained from the investigation of them it has been found possible to raise the mean fertility from 49.8 per cent. in 1937 to 68.1 in 1939 and 77.0 in 1940. By means of further improvements in diet and water temperature it would be possible to raise the fertility still higher.

It has been proved that Rainbow Trout are better suited to Jonkershoek conditions than Brown Trout.

ACKNOWLEDGMENTS.

In presenting this paper, which covers the results of four years' investigation, I wish to express my gratitude and appreciation to my Professor, Dr. C. G. S. de Villiers, of the University of Stellenbosch, for the interest which he has displayed in my work, his constructive criticism, and cordial co-operation.

I also wish to express my thanks and appreciation to Dr. C. L. Wicht for placing his data at my disposal and also for the loan of instruments; to Mr. F. G. Chaplin for the facilities extended to me during this investigation; and to the Department of Agricultural Chemistry of the Stellenbosch Elsenburg College of Agriculture for undertaking the qualitative analysis of the silt.

LITERATURE CITED.

1933. American Public Health Association and the American Water Works Association, Standard Methods of Water Analysis. (Seventh Edition.) New York.
1902. BENECKE, BERTHOLD.—Die Teichwirtschaft, s. 150. Vierte Auflage. Bearbeitet von S. Jaffe. Paul Parey, Berlin.
1932. BISSONNETTE, T. H.—"Modification of Mammalian Sexual Cycles," *Proc. Roy. Soc., Series B*, vol. 110, No. B.767, p. 322.
1923. COWLES, R. P., and SCHWITALLA, A. M.—"The Hydrogen Ion Concentration of a Creek, its Waterfall, Swamp and Ponds," *Ecology*, vol. 4, No. 4, p. 403.
1930. CREASER, CHARLES W.—"Relative Importance of Hydrogen Ion Concentration, Temperature, Dissolved Oxygen, and Carbon Dioxide Tension on Habitat Selection of Brook Trout," *Ecology*, vol. 11, No. 2, p. 246.
1921. EMBODY, G. C.—"High Water Temperature and Trout," *Salmon and Trout Mag.*, No. 44, p. 290.
1930. GEDDES, A. E. M.—*Meteorology*, p. 108. Blackie & Sons, London.
1940. GERRISH, STRATTON C.—"The Growth Rate of Brown Trout," *Salmon and Trout Mag.*, No. 99, p. 121.
1929. GUTSELL, JAMES S.—"Influence of certain water conditions, especially dissolved gases, on Trout," *Ecology*, vol. x, No. 1, p. 77.
1939. HEY, D.—"A Preliminary Report concerning the Causes of the Low Fertility of Trout Eggs at the Jonkershoek Trout Hatchery," *Annals of the University of Stellenbosch*, vol. 17, Section A, No. 1.
1940. HEY, D.—"A Further Report on the Low Fertility of Trout Eggs at the Jonkershoek Trout Hatchery," *Annals of the University of Stellenbosch*, vol. 18, Section A, No. 1.
1937. HOOVER, EARL E.—"The experimental modification of the Sexual Cycle in Trout by control of Light," *Science*, vol. 86, No. 2236, pp. 425-426.
1928. KREUZ, A.—*Teichbau und Teichwirtschaft*, p. 89. J. Neumann, Neudamm.
1914. KROGH, A.—"The Quantitative Relation between temperature and standard metabolism in Animals," *Intern. Zeit. Physik-Chem.*, pp. 491-508.
1916. NEEDHAM, JAMES C., and LLOYD, J. T.—*The Life of Inland Waters*. Comstock Publishing Company, Ithaca, New York.
1927. PHILIP, C. B.—"Diurnal Fluctuations in the Hydrogen Ion Activity of a Minnesota Lake," *Ecology*, vol. 8, No. 1, p. 73.
1923. POWERS, E. B.—"The Absorption of Oxygen by the Herring as affected by the Carbon Dioxide Tension of the Sea Water," *Ecology*, vol. 4, No. 3, p. 307.
1925. Rainfall Normals, 1925, and subsequent Annual Reports of the Chief Meteorologist of the Union of South Africa.
1927. RICHMOND, F. G.—"Acid Waters and the Salmonidae," *Salmon and Trout Mag.*, No. 46, p. 5.
1920. SMOLIAN, K.—*Merkbuch der Binnenfischerei*, Band 2. Deuter und Nicholas, Berlin.
1932. SOUTHERN, R.—"The Food and Growth of Brown Trout," *Salmon and Trout Mag.*, No. 67, p. 168.
1913. WARDLAW THOMPSON, W.—*The Sea Fisheries of the Cape Colony*. T. Maskew Miller, Cape Town.
1940. WICHT, C. L.—Unpublished Manuscript on Streamflow in Jonkershoek.
1939. WICHT, C. L.—"A Preliminary Account of Rainfall in Jonkershoek," reprinted from the *Trans. Roy. Soc. S. Afr.*, vol. 28, pt. 2.

The Council desires to acknowledge the receipt of a grant from the Cape Provincial Administration towards the cost of publication of this paper.

